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FISHERY BULLETIN

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SUPERSATURATION OF NITROGEN IN THE COLUMBIA RIVER AND ITS EFFECT ON SALMON AND STEELHEAD TROUT

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ABSTRACT

The nitrogen gas regime in the Columbia River was studied in 1966 (from Grand Coulee Dam, Wash., to the estuary at Astoria, Oreg.) and in 1967 (from Priest Rapids Dam, Wash., to the estuary). Dissolved nitrogen was subject to considerable seasonal fluctuation and varied with flow of water over spillways of dams; it was normal (near 100-percent saturation) in the fall and winter when no water was spilled, and high (above 135-percent saturation) in the spring and summer when large volumes of water were spilled. Some saturation levels over large areas were high enough and lasted long enough to be potentially dangerous to salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*).

Supersaturation of nitrogen at Priest Rapids Dam lowered the tolerance of juvenile fish to temperature increases, and some showed symptoms of gas bubble disease. Field studies to determine the effects of high levels of dissolved nitrogen on adult salmon and steelhead trout did not provide conclusive results.

Observations in the spring of 1965 by the Washington State Department of Fisheries and the Bureau of Commercial Fisheries showed that saturation of dissolved nitrogen at some sites in the Columbia River was as high as 125 percent. Because levels of this magnitude had produced gas bubble disease in adult and juvenile salmon (Rucker and Hodgeboom, 1953; Harvey and Cooper, 1962; and Westgard, 1964), additional surveys were made in 1966–67 to attempt to determine whether high levels of dissolved nitrogen might be responsible for losses of adult salmon and poor production of young fish at spawning channels.

The first phase in the study of nitrogen and oxygen concentrations (February–November 1966) was primarily to determine the cause of supersaturation of dissolved nitrogen and to determine seasonal variations. Water samples were taken from 26 sites between Grand Coulee Dam, Wash., near the Canadian border, and Astoria, Oreg., at the mouth of the river. The second phase (March–October 1967) was to determine the effect of nitrogen supersaturation on adult and juvenile salmon. We suspected that gas bubble disease was one of the factors in losses of adult and juvenile chinook salmon (*O. tshawytscha*) migrating between dams. The studies in 1967 concentrated on obtaining field evidence of such losses.

This report discusses the amounts of dissolved nitrogen in 1966–67, the effect of dams and reservoirs on saturation, the seasonal variation and duration of supersaturation, and the effect of supersaturation of nitrogen on juvenile and adult salmon and steelhead trout (*Salmo gairdneri*) in the Columbia River.

METHODS

Descriptions of the sampling stations, analytical techniques, and other experimental procedures are given in this section.

SAMPLING STATIONS AND TECHNIQUE

Twenty-six principal sampling stations were established along the Columbia River between the forebay of Grand Coulee Dam and the estuary at Astoria (fig. 1). All stations except 13, 25, and 26 were either in midreservoir, about 500 m. upstream from the dam, or on the spillway side of the river, about 500 m. below. Samples of water were taken at the surface and at 10-m. depths at the forebay stations. The spillways discharge from the surface down to a maximum depth of about 10½ m., and

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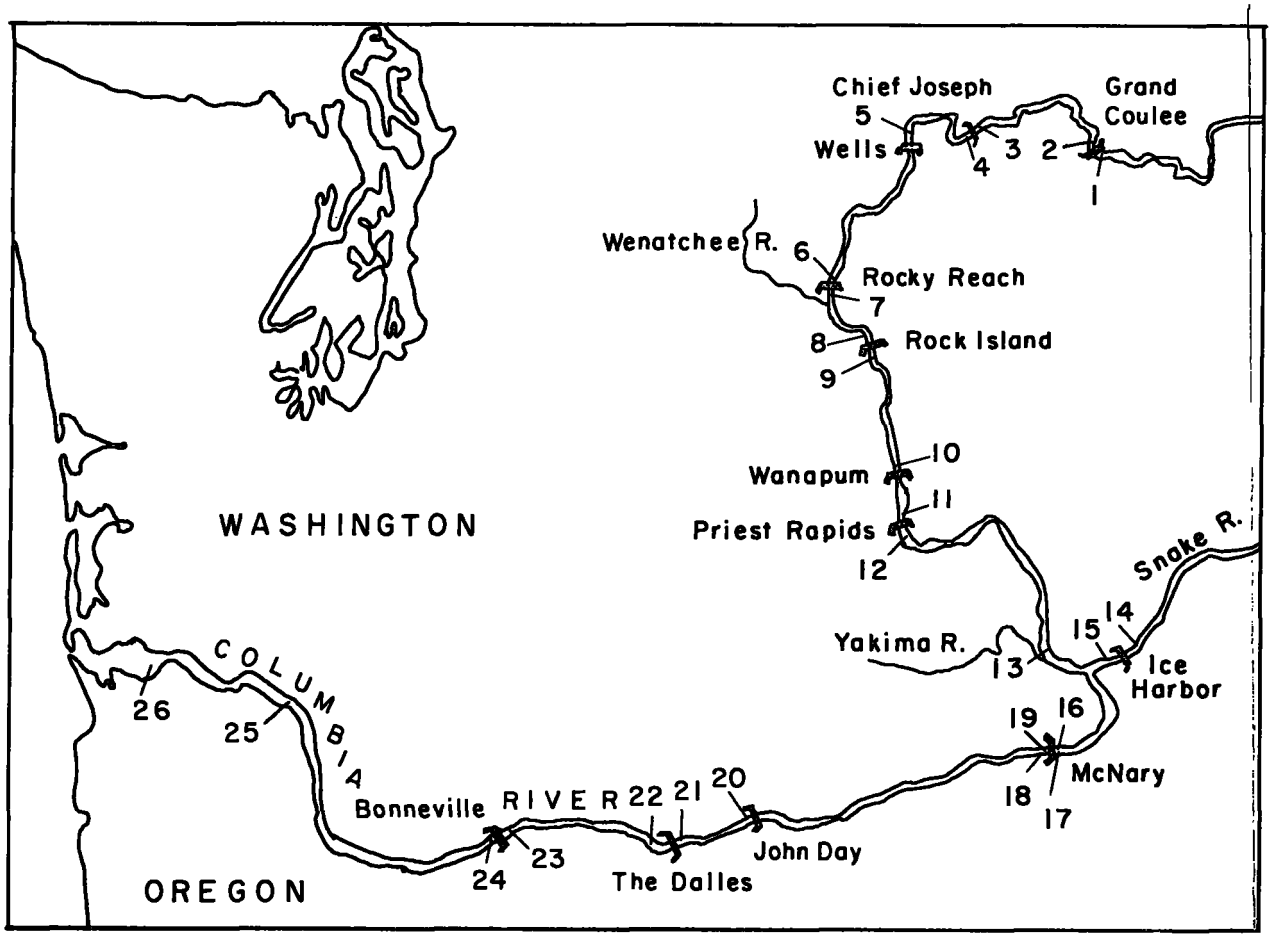

FIGURE 1.—Principal sampling stations on the Columbia and Snake Rivers.

the turbines withdraw water from about 8 m. down to 20 m. at all the dams downstream from Chief Joseph Dam. Maximum forebay depths at full pool do not exceed 45 m. Because of these facts and the fact that temperatures in the forebay of the reservoirs seldom varied more than 1° C. from the surface to the bottom, a sample at the surface and 10-m. depth was sufficient to represent the average forebay concentration and in turn represent the water passing through the turbines and spillways. Duplicate samples were collected at the surface at stations below the dams where high current velocities made it impossible to sample at depth. Because the amount of soluble nitrogen depends on water temperature,[1] the temperature of each sample was recorded before it was placed in an iced cooler for transport to the laboratory. The use of two aircraft made it possible to obtain all samples in 1 day; analysis was completed on the following day.

Water samples were obtained from additional stations when more information was needed for a specific dam or reservoir. For example, additional stations were established along the reservoirs behind McNary and Chief Joseph Dams to study changes in nitrogen content of water passing through these reservoirs. Additional stations were also sampled when the effect of a specific dam on saturation levels was examined. Table 1 gives a detailed description of the principal sampling stations and the dates when samples were obtained.

ANALYSIS

The amount of dissolved nitrogen in the sample was determined by a modification of the technique used by Swinnerton, Linnenbom, and Cheek (1962). A Fisher blood gas analyzer Model

[1] An atmospheric pressure of 760 mm. mercury was used in computing normal saturation (100 percent) for each sample.

TABLE 1.—*Locations and dates of sampling in the Columbia and Snake Rivers; sampling sites are shown by number in figure 1*

Station location and number		Dates sampled																				
		1966										1967										
		Feb. 9	Mar. 7	Apr. 6	Apr. 18	May 9	June 6	July 11	Aug. 1	Sept. 6	Oct. 2	Nov. 7	Apr. 3	May 1	May 15	June 6	June 27	July 5	July 19	Aug. 2	Aug. 23	Sept. 5	Oct. 3
Number	*Station*																					
1	Forebay—Grand Coulee Dam.	X	X	X	X	X	X	X	X	X	X	X	----									
2	Tailrace—Grand Coulee Dam.	X	X	X	X	X	X	X	X	X	X	X	----									
3	Forebay—Chief Joseph Dam.	X	X	X	X	X	X	X	X	X	X	X	----									
4	Tailrace—Chief Joseph Dam.	X	X	X	X	X	X	X	X	X	X	X	----									
5	Wells damsite	X	X	X	X	X	X	X	X	X	X	X	----									
6	Forebay—Rocky Reach Dam.	X	X	X	X	X	X	X	X	X	X	X	----									
7	Tailrace—Rocky Reach Dam.	X	X	X	X	X	X	X	X	X	X	X	----									
8	Forebay—Rock Island Dam.	X	X	X	X	X	X	X	X	X	X	X	----									
9	Tailrace—Rock Island Dam.	X	X	X	X	X	X	X	X	X	X	X	----									
10	Forebay—Wanapum Dam.	X	X	X	X	X	X	X	X	X	X	X	----									
11	Forebay—Priest Rapids Dam.	X	X	X	X	X	X	X	X	X	X	X	----				X	X	X	X	X	----
12	Tailrace—Priest Rapids Dam.	X	X	X	X	X	X	X	X	X	X	X	----				X	X	X	X	----	
13	Columbia River at Richland, Wash.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
14	Forebay—Ice Harbor Dam.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	----	X	----	X
15	Tailrace—Ice Harbor Dam.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	----			
16	Forebay—McNary Dam (north side).	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
17	Forebay—McNary Dam (south side).	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
18	Tailrace—McNary Dam (south side).	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
19	Tailrace—McNary Dam (north side).	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
20	John Day damsite	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
21	Forebay—The Dalles Dam.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
22	Tailrace—The Dalles Dam.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
23	Forebay—Bonneville Dam.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	----
24	Tailrace—Bonneville Dam.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	----
25	Columbia River at Longview, Wash.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
26	Columbia River estuary Astoria, Oreg.	X	X	X	X	X	X	X	X	X	X	X	X	----								

6–390V2 [2] was substituted for their Model 25, and the length of the extraction chamber was increased to 150 mm. Model 6–390V2 is more sensitive than Model 25, and the longer extraction chamber allowed analysis of larger samples.

Saturation values quoted in this report are correct to within ±2 percent. Limitations in the accuracy of the method and the uncertainty of the theoretical solubilities of nitrogen precluded more precise interpretation.

[2] Trade names referred to in this publication do not imply endorsement of commercial products by the Bureau of Commercial Fisheries.

EFFECT OF DAMS AND RESERVOIRS ON SATURATION OF DISSOLVED NITROGEN

Major causes of supersaturation of water with gases are heavy concentrations of algae (Woodbury, 1942), warming of water without adequate circulation and exposure to the atmosphere for equilibration, and falling of water into an enclosed plunge basin (Harvey and Cooper, 1962). Algae concentrations like those described by Woodbury are not found in the Columbia River and the river is not warmed sufficiently at any location to account for the high concentrations previously recorded. Spillways at dams create

conditions similar to those described by Harvey and Cooper and were suspected to be the major cause of supersaturation; during periods of high flow, large volumes of water plunge from spillways at all the dams on the Columbia River into various types of basins.

OBSERVATIONS AT DAMS

Samples analyzed at individual dams to determine the effect of turbines and spillways on dissolved nitrogen indicated that supersaturation in the Columbia River is caused primarily by spillways. This was clearly demonstrated during tests at Bonneville Dam in March 1966 when the Corps of Engineers spilled large volumes of water at a time when spilling normally does not occur. Variables, such as spilling at upstream dams and rapid temperature increases, were eliminated; the only factor which remained that could create supersaturation was the spilling of the water. The concentration of dissolved nitrogen at Bonneville Dam before and during these spillway tests is shown in figure 2. Two replicates of samples were taken before spill and three replicates after spill at each location. Maximum variance in analysis at each location before spill was 4 percent; after spill, 6 percent. Concentrations in the forebay and below the turbines and spillway before the spill tests were near normal saturation (98–102 percent). During the spill tests, concentrations below the spill increased to 125-percent saturation, whereas concentrations in the forebay and below the turbines remained near 100 percent.

Nitrogen levels at other dams (table 2) indicated that each dam has different, characteristic effects on nitrogen saturation. The spillways at Bonneville, Grand Coulee, and Ice Harbor Dams increased the concentration of nitrogen, but the amount of the increase differed. By contrast, the spillway at Priest Rapids decreased the concentration when the water was supersaturated above the dam. Differences in the structural arrangement of the dams, shape of the spillways, and depth of tailwater are factors which could explain the differences.

EQUILIBRATION IN RESERVOIRS

Sampling throughout the length of reservoirs above Chief Joseph and McNary Dams showed that water supersaturated with dissolved nitrogen does not equilibrate during transit. In McNary Reservoir on June 8, the saturation of nitrogen that entered the reservoir from the Columbia River averaged 127 percent; samples collected in the forebay of McNary Dam on the same day averaged 127 percent. Evidently, lack of circulation and warming of the surface water in the forebay tended to maintain the saturation level.

TABLE 2.—*Average nitrogen concentrations (percentage saturation) in the Columbia River of samples taken at specific dams to determine effect of dams on water passing through turbines and over spillways (spring 1966)*

Location and date	Forebay above spill	Tailwater below spill	Forebay above turbines	Tailwater below turbines	Samples	Spill volume
	Percent	*Percent*	*Percent*	*Percent*	*Number*	*100 c.m.s.*
Bonneville:						
Mar. 10 and 11	102	125	94	98	8	28.3–42.5
The Dalles:						
Feb. 27–Mar. 2	103	104	102	97	12	1–33.7
Ice Harbor:						
May 16 and 18	109	118	107	105	8	.5–0.8
Priest Rapids:						
May 25 and 31	131	114	121	.....	8	1.9–2.4
Grand Coulee:						
Apr. 27	105	129	105	105	4	.7

SEASONAL AND DAILY VARIATIONS IN SATURATION OF DISSOLVED NITROGEN

As expected, variations of dissolved nitrogen concentrations from Grand Coulee Dam to the estuary depended largely on the volume of water released over the spillways. Nitrogen saturation in February, March, and April of 1966 was below 110 percent except below dams where intermittent spilling occurred. On February 9, when no dams were spilling (table 3), all samples had saturation below 105 percent (fig. 3). The concentrations in March were nearly the same except below the Bonneville spillway where spilling was minimal. Saturation of dissolved nitrogen remained below 110 percent through April except in areas of spilling. Streams began to rise in April, and spill releases became regular at all dams by early May. Surface concentrations of nitrogen were over 110 percent at all stations except in the forebay of Grand Coulee and The Dalles Dams. The highest concentration in May (132 percent) was downstream from the spillway at Bonneville Dam. Temperature on May 9 ranged from a low of 8.5° C. (47.3° F.) in the forebay of Chief Joseph Dam to a high of 15.3° C. (59.5° F.) in the forebay of Grand Coulee Dam.

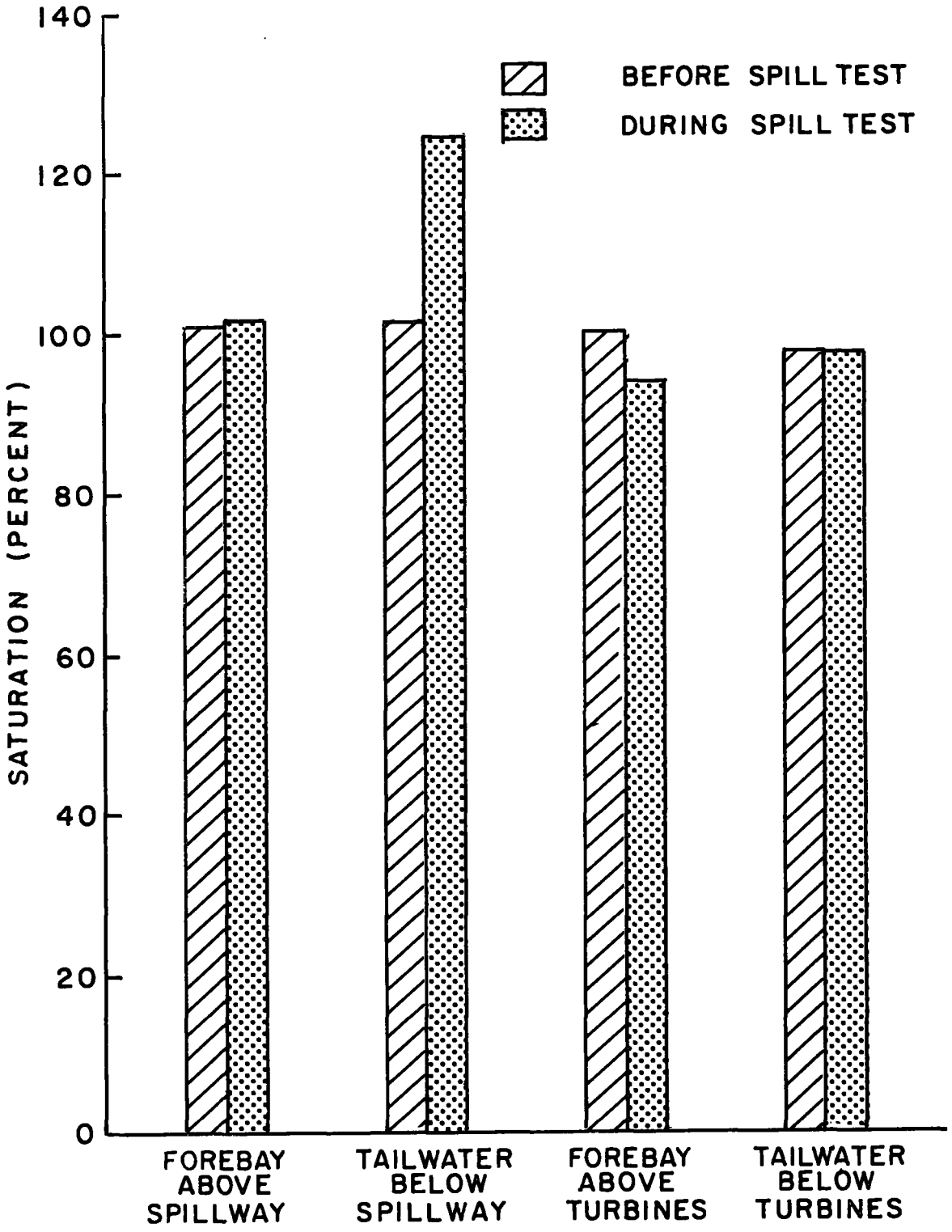

FIGURE 2.—Percentage saturation of dissolved nitrogen in 32 samples taken near Bonneville Dam before and during spill tests, March 3–11, 1966.

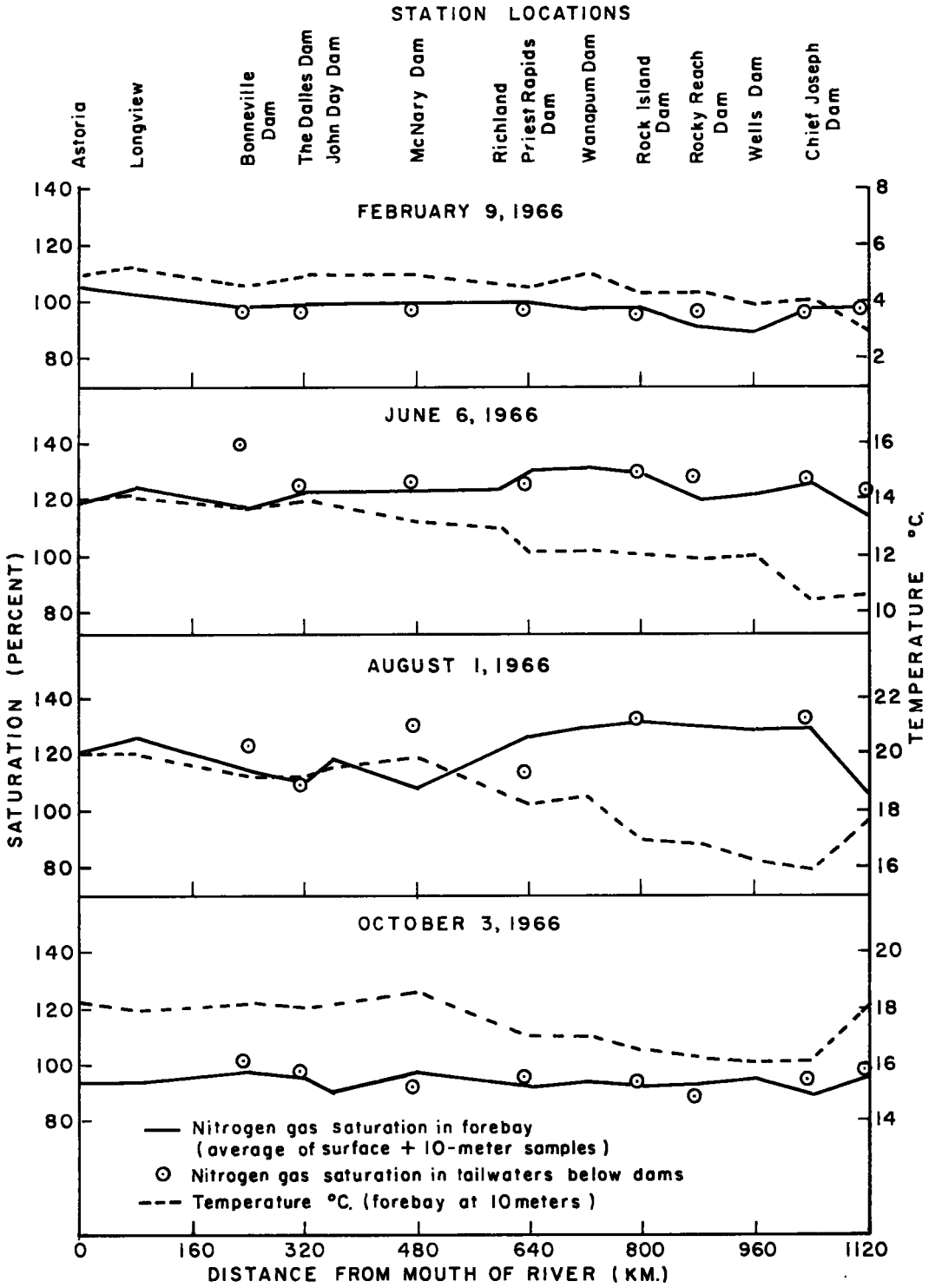

FIGURE 3.—Saturation of dissolved nitrogen and temperature of samples in Columbia River from Astoria to Grand Coulee Dam, February to October 1966.

TABLE 3.—*Mean daily spill (S.) and total flow (T.), in 100 c.m.s. (hundreds of cubic meters per second), at different Columbia River dams, February–November 1966*

Dam	Feb. 9		Mar. 7		Apr. 6		May 9		June 6		July 1		Aug. 1		Sept. 6		Oct. 3		Nov. 7	
	S.	T.	S.	T.	S.	T.	S.	T.	S.	T.	S.	T.	S.	T.	S.	T.	S.	T.	S.	T.
	100 c.m.s.																			
Grand Coulee	0.0	21.8	0.0	21.9	0.0	17.5	19.4	47.2	55.1	74.7	49.7	66.3	22.4	42.9	0.0	19.5	0.0	21.0	0.0	18.4
Chief Joseph	.0	23.2	.0	26.1	.0	15.1	28.8	47.5	60.3	77.9	48.1	71.1	20.7	41.4	.0	22.6	.0	20.6	.0	16.5
Rocky Reach	.0	23.7	.0	22.4	.0	16.5	------	52.0	------	78.1	------	68.5	------	43.6	.0	22.0	.0	20.1	.0	17.5
Rock Island	.0	24.3	.0	23.2	.0	17.4	------	57.7	------	83.5	------	73.3	------	45.4	.0	22.3	.0	20.5	.0	17.5
Wanapum	.0	24.7	.0	27.1	.0	19.4	17.1	54.3	46.0	80.8	31.9	69.2	1.9	44.8	.0	23.1	.0	23.5	.0	22.1
Priest Rapids	.0	25.4	.0	26.9	.0	19.4	21.9	56.2	46.8	81.4	36.3	70.3	36.2	35.7	.0	23.2	.0	23.6	.0	21.5
Ice Harbor	.0	7.1	.0	19.3	.0	19.3	19.3	30.9	9.7	21.0	.0	7.2	.0	6.1	.0	6.2	.0	4.5	.0	6.1
McNary	.0	31.7	.0	26.4	.0	42.8	50.7	91.4	56.7	99.4	41.7	79.1	11.1	54.1	.2	24.6	.0	25.3	.0	25.7
The Dalles	.0	33.0	.0	27.1	.0	46.4	43.4	84.1	60.3	101.0	39.3	80.3	11.5	57.6	.0	26.7	.0	25.3	.0	26.2
Bonneville	.0	33.7	.0	24.3	.0	44.9	59.6	86.5	67.8	99.6	47.3	80.1	23.8	56.6	.0	27.8	.7	26.1	.0	26.6

The highest nitrogen saturation during 1966 occurred in June. Concentrations ranged from 112 to 140 percent; most of the samples were above 120 percent (fig. 3). These values remained high through August between Grand Coulee and Priest Rapids Dams. On July 11 and August 1, however, the river equilibrated rapidly between Priest Rapids and McNary Dams. Concentrations in the forebays dropped from an average of 132 percent at Priest Rapids Dam to an average of 109 percent at McNary Dam. Spilling at Bonneville Dam then increased the saturation to above 120 percent downstream from Bonneville. The rapid equilibration of gas content between Priest Rapids and McNary Dams during July and August was probably caused by the increased circulation of water in the unimpounded river area below Priest Rapids and the lower total flow and spill volumes at Priest Rapids and Ice Harbor Dams (table 3).

In September, Columbia River flows had decreased further and spilling had almost ceased at all dams; this change precipitated a marked reduction in the saturation of nitrogen at all stations—only five samples were above 110 percent. Saturation continued to decrease in October and was well below 110 percent—ranging from 88.4 percent at Rocky Reach Dam to 100.6 percent at Grand Coulee Dam. Water temperatures in October ranged from 16.1° to 18.6° C. (60.8–65.5° F.), and the average temperature was about 1° C. lower than in September. The lack of spilling and lower water temperatures accounted for the decrease in saturation from August to September.

In the last survey during 1966, on November 7, the saturation was not significantly different from that in October 1966 (or November 1965).

DIURNAL VARIATIONS

During a 24-hour period (June 30 and July 1, 1966) of moderately high saturation in the forebay of The Dalles Dam, nitrogen concentrations varied only 0.6 p.p.m. from a maximum of 18.6 p.p.m. (114 percent saturation). Spill volumes at The Dalles Dam were nearly constant for the 24-hour period.

SEASONAL VARIATIONS IN THE SNAKE RIVER

Samples from the tailrace below the spillway of Ice Harbor Dam in the Snake River (station 15) indicated a seasonal variation in amount of nitrogen similar to that in the Columbia River; i.e., normal saturation before spill releases increased saturation as spill releases increased and decreased saturation as spill releases subsided. The timing of the cycle differed from that in the Columbia River, as spilling at Ice Harbor Dam usually began in late April, peaked about mid-May, and ended by mid-June. Thus, the net effect of the Snake River discharge on saturation in the Columbia River was to increase the amount of nitrogen in late April and May and decrease it in June, July, and August.

COMPARISION OF 1966 AND 1967

Saturation of dissolved nitrogen in 1967 followed the same general seasonal changes as in 1966. Values were normal in winter and early spring before the dams began spilling, but rose as spilling increased. Levels again were highest in June and July when the largest volume of water passed through the spillways. When spilling ceased and cooling of the river began in September and October, saturation decreased sharply (fig. 4).

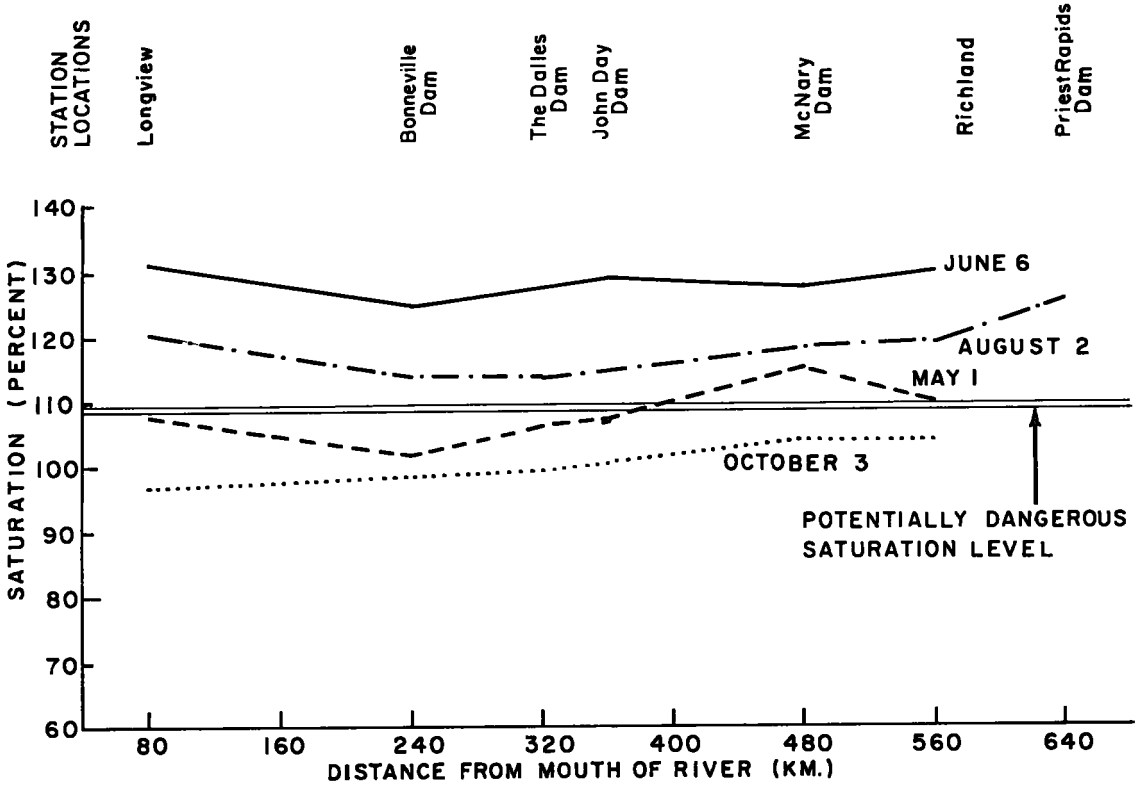

FIGURE 4.—Saturation values of dissolved nitrogen in samples of Columbia River water taken from Longview, Wash., to Priest Rapids Dam, May 1, June 6, August 2, and October 3, 1967. (Values shown are the averages of the surface and 10-m. sample at each location.)

Saturation in May 1967 (102–115 percent) was considerably lower than in May 1966 (110–133 percent) because spillway releases in 1967 were not significant on the main Columbia until late May. By mid-June 1967, however, extremely high spillway releases brought even higher saturations than were recorded in 1966.

In 1966–67 the saturation of dissolved nitrogen over a large area of the river was sufficiently high and of sufficient duration (middle to late May through mid-August) to be a potential danger to migrating juvenile and adult salmon and trout. Experiments by Westgard (1964) showed that adult chinook salmon held in water with concentrations of dissolved nitrogen at 116 percent saturation developed definite symptoms of gas bubble disease. Harvey and Smith (1962) indicated that saturation as low as 108 percent produced gas bubble disease in fingerlings at Cultus Lake Trout Hatchery. These values were much lower than those recorded in the Columbia River. The fish were held in shallow ponds or raceways, however, whereas fish in the Columbia River are usually able to move to greater (compensating) depths, except when they are ascending fishways. The ability of fish to seek compensating depths must be taken into account in the assessment of the effect of high saturation of nitrogen in the Columbia River.

EFFECT OF SUPERSATURATION OF DISSOLVED NITROGEN ON SALMON IN THE COLUMBIA RIVER

Studies of supersaturation of nitrogen in 1967 were made in conjunction with tagging studies designed to determine the cause of loss of adult fish during their migration from Bonneville to Ice Harbor and Priest Rapids Dams.[3] The primary purpose in 1967 was to determine the effect of dissolved nitrogen on juvenile and adult salmon and steelhead known to be in the river when concentrations of dissolved nitrogen were high.

[3] Tagging study in progress by Bureau of Commercial Fisheries, Seattle, Wash.—James H. Johnson, Program Leader.

JUVENILE SALMON

Examination of juvenile chinook salmon that suffered excessive mortality in holding tanks (used for marking fish) at Priest Rapids Dam in 1966 revealed that most fish had symptoms of gas bubble disease. Although the fish otherwise appeared to be sound, they were definitely distressed and, if held, eventually died from gas embolism. Dissolved nitrogen concentrations at Priest Rapids Dam ranged from 114 to 133.9 percent saturation. Temperature in the gatewells of the dam from which fish were collected ranged from 13.9° C. (57° F.) on July 7 to 17.8° C. (64.0° F.) on August 31 when operations ceased. The water temperature in the holding tanks usually rose about 1° to 2° C. before marking began. This slight increase was sufficient to liberate enough gas from the blood of the fish to cause embolism and death. The symptoms of gas bubble disease and distress were eliminated if these fish were held in water slightly cooler than that in the river where they were collected. Usually a decrease of 1° or 2° C. was sufficient to reduce the mortality.

Apparently, juvenile chinook salmon, equilibrated to supersaturation of nitrogen in this temperature range, have considerably less tolerance to increases in temperature than fish that are equilibrated to normal saturation. Brett (1952) in his studies of the tolerance range of juvenile salmon to temperature changes showed that spring chinook salmon acclimated to 10° C. (50° F.) could tolerate temperatures up to 24.5° C. (76.1° F.) before mortalities began. The fish at Priest Rapids Dam, which were acclimated to higher temperatures (13.9–17.8° C.), could not tolerate increases of 1° to 2° C.

It was apparent from observations at Priest Rapids Dam that juvenile migrants were in a precarious situation in July and August. If they did not remain at sufficient depth to compensate for the supersaturation of dissolved nitrogen, they died of gas bubble disease. Their tolerance to temperature increases was also lowered; conceivably sudden temperature increases of only a few degrees centigrade would have caused mortality.

We conducted an experiment in the forebay of Priest Rapids Dam to determine the depth at which juvenile fish must remain to avoid gas bubble disease when subjected to supersaturation of nitrogen. Juvenile coho (*O. kisutch*) and chinook salmon were held in pens submerged at different depths in the forebay and then observed by SCUBA divers at various intervals for symptoms of gas bubble disease. Three tests from 200–280 hours' duration were conducted from May 28 to August 14, 1967, a period when saturation of dissolved nitrogen changed from a high of 143 percent in late May and June to 118 percent in August. Hatchery-reared coho salmon were used in tests 1 and 2 and wild chinook in test 3. One hundred fish were placed in each test cage and in a control cage held in river water of normal saturation at the dam. The first observation was made about 12 hours after placing the cages at the selected depths in the forebay. Other observations were made at 24-hour intervals for the first 4 days; the time between observations was increased thereafter, depending on rate of mortality. Dead fish were brought to the surface by divers and examined for symptoms of gas bubble disease. Neither test nor control fish were fed during the tests. In one test 100 percent of the coho salmon in a surface pen and 70 percent in a pen lowered to a depth of 2 to 3 m. died from gas bubble disease (fig. 5). Three percent was the maximum mortality for control fish held during the test. The experiment showed that at 130 to 140 percent saturation fish must remain below 2.5 m. if they are to be free of symptoms of gas bubble disease. From

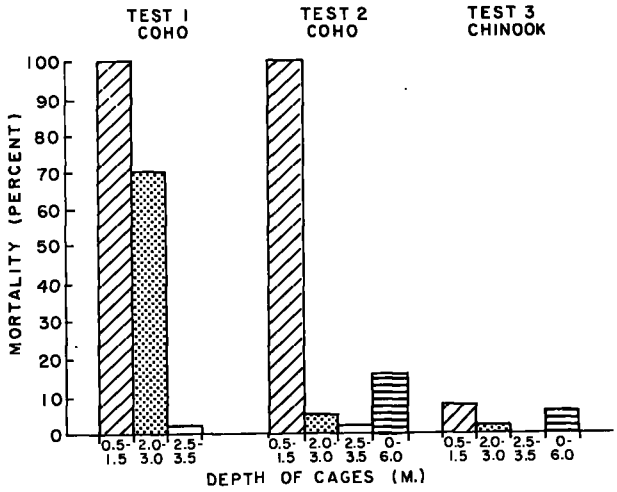

FIGURE 5.—Percentage mortality caused by gas bubble disease during holding experiment in forebay of Priest Rapids Dam May 28 to August 14, 1967. Saturation of dissolved nitrogen ranged from 143 percent in test 1 to 118 percent in test 3; fish were held about 200 hours in tests 1 and 2,280 hours in test 3.

6 to 16 percent of the coho and chinook salmon died in a pen which allowed the fish to seek any depth from the surface to 6 m., which suggested that some mortality may also have occurred to naturally migrating fingerlings even though they could move to any depth.

These field observations of juvenile migrants, though limited, indicate that naturally migrating juvenile fish in the Priest Rapids Dam area are under stress from supersaturation of dissolved nitrogen; it is highly probable that a significant percentage of the fish is lost. The Hanford area of the river downstream from Priest Rapids is of particular concern. Juvenile and adult salmon already under stress must pass areas where thermal reactors emit large volumes of water with temperatures 10° to 15° C. higher than the river temperatures. Obviously, fish under stress from supersaturation of gases have less tolerance to rapid temperature increases, and losses of fish which inadvertently enter the thermal plumes are inevitably high. Further investigation seems imperative on the effect of supersaturation of dissolved nitrogen on the tolerance of salmon to temperature increases.

ADULT SALMON AND STEELHEAD TROUT

About 2,300 adult chinook salmon, 1,600 steelhead trout (*Salmo gairdneri*), and 1,000 sockeye salmon (*Oncorhynchus nerka*) were examined at Bonneville and McNary Dams from mid-April through mid-October 1967 for external symptoms of gas bubble disease. The external symptoms that were used to indicate gas bubble disease were (1) gas bubbles under skin, in roof of mouth, and in fin membranes and (2) hemorrhaging inside the eye and the associated "pop eye" condition of the eyeball. Nitrogen saturation was measured at both dams so that the incidence of disease symptoms could be correlated with the saturation of nitrogen.

Examination of the adult salmon and steelhead trout began on April 11 when saturation was about 106 percent and continued until May 25 when saturation was near 120 percent. Because nitrogen saturation did not exceed 110 percent until May 10, little incidence of gas bubble disease was expected; 1 of 125 steelhead trout examined showed symptoms of the disease (on May 25).

Observations of adult fish at McNary Dam began on June 23 and ended October 11. Nitrogen saturation ranged from 131 percent in June to 104 percent in October. Saturation was high (above 120 percent) from June 23 to July 19 but began to drop sharply after July 19; by August 22, values were below 110 percent. In July, symptoms of gas bubble disease were noted in 10 of 1,000 sockeye salmon, but none were observed in 1,762 chinook salmon and 1,461 steelhead trout. Apparently, chinook salmon and steelhead trout in this area either compensated for the high saturation by remaining at a sufficient depth or the symptoms of the disease had not progressed sufficiently to be evident.

Surveys for carcasses of adult fish were made from April to October during each flight made to obtain water samples. Four additional aerial surveys for carcasses were made during June and July when saturation was highest. Carcasses of eight dead salmon (and a few unidentified fish) were observed; however, it could not be positively verified that any of these fish had died from gas bubble disease. Generally, the fish were too decomposed for determination of cause of death.

Steelhead trout and chinook salmon were observed (June 15 to September 19) congregating in the Columbia River at its confluence with the Snake River. Saturation of dissolved nitrogen in the Columbia ranged from 110 to 130 percent, and temperatures in the Snake River were as much as 5.7° C. (10.3° F.) higher than in the Columbia (table 4). Fish equilibrated to supersaturation of dissolved nitrogen in the Columbia could have died from gas embolism if they had entered the Snake River at this time. A concentrated search on the surface by boat and on the bottom with SCUBA did not yield carcasses of any salmon whose death

TABLE 4.—*Temperature (° C.) and percentage saturation of dissolved nitrogen in the Columbia and Snake Rivers at the mouth of the Snake River—June 6 to Sept. 5, 1967*

Date	Columbia River at mouth of Snake River		Snake River at mouth	
	Temperature	Saturation of dissolved nitrogen	Temperature	Saturation of dissolved nitrogen
	° C.	*Percent*	*° C.*	*Percent*
June 6	13.2	130	12.2	126
June 27	14.2	129	16.3	123
July 5	16.6	129	19.4	113
July 19	17.0	126	22.2	.....
July 27	18.4	120	23.0	109
Aug. 2	19.1	119	23.7	111
Aug. 9	19.3	118	25.0	108
Aug. 15	21.0	118	24.7	106
Aug. 30	20.3	118	23.5	103
Sept. 5	21.2	110	23.3	105

could be attributed to gas bubble disease or gas embolism. A study of the movement of these fish indicated that many did not reach Ice Harbor Dam.[4] The destination or fate of these fish was not determined.

We have no positive evidence to indicate that the high nitrogen saturation in the Columbia River in 1967 caused serious mortality of adult salmon, but the possibility cannot be discounted. From the surveys and searches made in 1967 it was obvious that it would be difficult to detect a continuous low rate of mortality in a river the size of the Columbia even with continuous surveillance. Various reports of mortality were received from local residents, but again it could not be established that fish had died from gas bubble disease.

SUMMARY AND CONCLUSIONS

A seasonal cycle of supersaturation of dissolved nitrogen occurs each year in the Columbia River. Degree of supersaturation varies with flow of water over spillways of dams. Levels are normal (near 100-percent saturation) in the fall and winter when little or no spilling takes place and high (above 120 percent) in the spring and summer when large volumes of water are being spilled. Water plunging over spillways is the primary cause of supersaturation in the Columbia River.

Water supersaturated with nitrogen does not equilibrate rapidly in reservoirs. Lack of circulation and increases in surface water temperature tend to slow the rate of equilibration. Saturation of dissolved nitrogen in the Columbia River is sufficiently high and occurs over a large area over a sufficiently long time to be potentially dangerous to salmon and steelhead trout. Observations of juvenile salmon at Priest Rapids Dam indicate that supersaturation of nitrogen offers a definite problem; further study is needed to determine its extent.

Field observations to determine the effect of high levels of dissolved nitrogen on adult salmon and steelhead trout were not conclusive. Some sockeye salmon and steelhead trout were observed with symptoms of gas bubble disease, but no chinook salmon had symptoms. A potential problem exists for adult salmon and trout migrating from the Columbia River into the Snake River in July and August. Fish equilibrated to supersaturation of nitrogen from the Columbia River encounter an increase of 5° to 6° C. in temperature on entering the Snake River. The tolerance of the salmon to this temperature change under those conditions is unknown.

[4] Percentage of tag returns from fish subjected to these conditions was *about 50 percent lower than returns from other groups* passing over Ice Harbor Dam. (Verbal communication, Gerald Monan, BCF Biological Laboratory, Seattle, Wash.)

ACKNOWLEDGMENTS

I thank Richard Westgard of the Washington Department of Fisheries for providing photos of external symptoms of gas bubble disease in adult chinook salmon and for his advice on analytical techniques for dissolved nitrogen. I also thank Richard Krema of the Bureau of Commercial Fisheries, Pasco, Wash., for his help in conducting the holding experiment at Priest Rapids Dam.

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ADDITIONS TO A REVISION OF ARGENTININE FISHES

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ABSTRACT

Four new species of the genus *Argentina* are described, three from the western Atlantic and one from Peru. Range extensions are presented for *A. euchus* from the western Indian Ocean and *A. sialis* from the northeastern Pacific. Speciation in the genus is discussed, and a key is presented to the 12 species recognized. Pigmentation of the swimbladder and its significance as a systematic character are discussed.

A new species of *Glossanodon* from the western Indian Ocean is described, and additional material of *G. polli* from the tropical eastern Atlantic is noted.

Argentinine fishes are taken in commercial quantities in the temperate western North Atlantic (Emery and McCracken, 1966) and are forage fishes in Australia (Fairbridge, 1951). Species found in tropical waters are usually associated with shrimp grounds and are available to shrimp fishing gear. This paper supplements the revision of argentinine fishes published by Cohen in 1958. Since then, additional material has accumulated comprising undescribed species, additional material of poorly known forms, and range extensions. In this paper we reassess the status of populations in the genus *Argentina*. We discuss speciation, comment on swimbladders, and describe one new species from Peru and three from the tropical western Atlantic. Range extensions are recorded for *A. euchus* from the western Indian Ocean and *A. sialis* from the northeastern Pacific. A new species of *Glossanodon* from the western Indian Ocean is described, and additional material of *G. polli* from tropical West Africa is noted.

MATERIALS AND ACKNOWLEDGMENTS

We have received material from the Smithsonian Oceanographic Sorting Center; the U.S. Program in Biology of the International Indian Ocean Expedition; the Guinean Trawling Survey; the Southeastern Pacific Biological and Oceanographic Program; the Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Bases at Pascagoula, Miss., and Seattle, Wash.; and Scripps Institution of Oceanography.

Specimens stored in the following collections have been examined: U.S. National Museum, Wash., D.C. (USNM); Harvard Museum of Comparative Zoology, Cambridge, Mass. (MCZ); Field Museum of Natural History, Chicago, Ill. (FMNH); Stanford University Division of Systematic Biology, Stanford, Calif. (SU); Scripps Institution of Oceanography, La Jolla, Calif. (SIO); British Museum, Natural History, London (BMNH); Museum National d'Histoire Naturelle, Paris (MNHN); Universitetets Zoologiske Museum, Copenhagen (UZMC); University of Miami Marine Laboratory, Miami, Fla. (UMML); Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Fla. (TABL); Academy of Natural Sciences, Philadelphia, Pa. (ANSP); Tulane University, New Orleans, La. (TU); University of Florida, Gainesville, Fla. (UF); Gulf Coast Research Laboratory, Ocean Springs, Miss. (GCRL); and California Academy of Sciences, San Francisco, Calif. (CAS).

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We thank the curators of the collections listed above for allowing us to examine specimens in their care and providing X-ray photographs. We also thank the many individuals in the field programs listed above who have helped us.

METHODS

Methods and definitions follow Cohen (1958). We note in particular that the split posterior ray of the dorsal and anal fins is counted as two rays and that the vertebral count does not include the urostyle or the hypural fan. The method of counting gill rakers is shown in figure 1. Meristic characters are given as the mode followed by the range in parentheses. Where the range includes data for more than one species, no mode is given. Measurements are given as the mean followed by the range in parentheses.

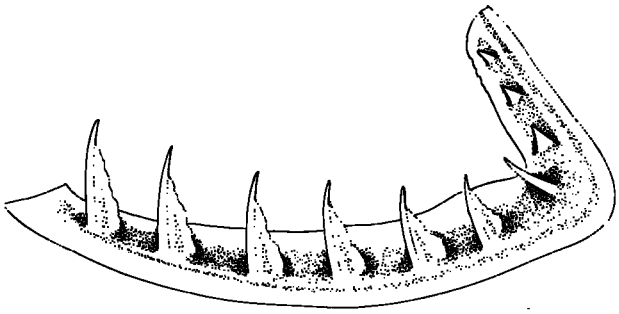

FIGURE 1.—*Argentina striata*, USNM 203001. First gill arch from left side; rakers on lower arm are counted as six. Gill filaments are not shown. Drawn by Mildred H. Carrington.

GENUS *ARGENTINA* LINNAEUS

For this genus, we divide the species into two groups and discuss sympatry and its significance, taxonomic significance of the swimbladder, and present a key to the species of *Argentina*.

SPECIES GROUPS

The 12 species of *Argentina* are divided into two groups.

Species Group 1

Four species are in this group. They are *silus* and *sphyraena* from the North Atlantic and Mediterranean and *sialis* and *aliceae* from the eastern Pacific. This group is distinguished by its larger jaw, almost always greater than 21.5 percent of head length (fig. 2), and usually more gill rakers (7–21 on the lower arm of the first gill arch; one species, *A. sphyraena*, has few gill rakers, 7–10, but the other three species have 11–21; see table 1). The species in this group are allopatric (although the gross geographical ranges of *sphyraena* and *silus* overlap, they are ecologically separate, mainly living and certainly spawning at different depths), and are very distinct morphologically.

Species Group 2

Eight species are in this group. They are *striata*, *brucei*, *georgei*, and *stewarti*, all from the western Atlantic; *euchus*, from the western Indian Ocean; and *elongata*, *australiae*, and *kagoshimae* from the western Pacific. This group is distinguished by its shorter jaw, almost always less than 20 percent of head length, and generally fewer gill rakers (5–10, but one species, *A. elongata*, has more gill rakers, 8–10; the other species have 5–8). At least some of the species in this group are sympatric.

SYMPATRY AND ITS SIGNIFICANCE

Cohen (1958) treated the forms (then three, a fourth is described in this paper) constituting the *silus* group as full species. However, the three western Pacific forms of the *striata* group, *australiae*, *elongata*, and *kagoshimae*, were recognized as subspecies because these disjunct populations (Australia, New Zealand, and Japan, respectively) are very similar to each other, far more so than are the species in the *silus* group (see key). *A. striata* was recognized as a full species, but could just as easily have been ranked as a subspecies. *A. euchus* (Cohen, 1961) was given full species rank because it was described from only two specimens.

Subsequent study of hundreds of specimens from the western Atlantic has shown that what was formerly considered to be a single species, *A. striata*, clearly comprises four forms. These forms are similar to each other and separated by few characters. In fact, they are distinguished, one from the other, by characters which both qualitatively and quantitatively resemble those that separate the western Pacific forms.

We recognize the four closely related western Atlantic forms as full species because at least some of them are sympatric. *A striata* and *brucei* have been taken together in trawl hauls off Venezuela (*Atlantis* sta. 2700; *Oregon* sta. 1989, 4410, and 4465). *A. brucei* and *stewarti* were taken together off Nicaragua (*Oregon* sta. 3574 and 3610). *A.*

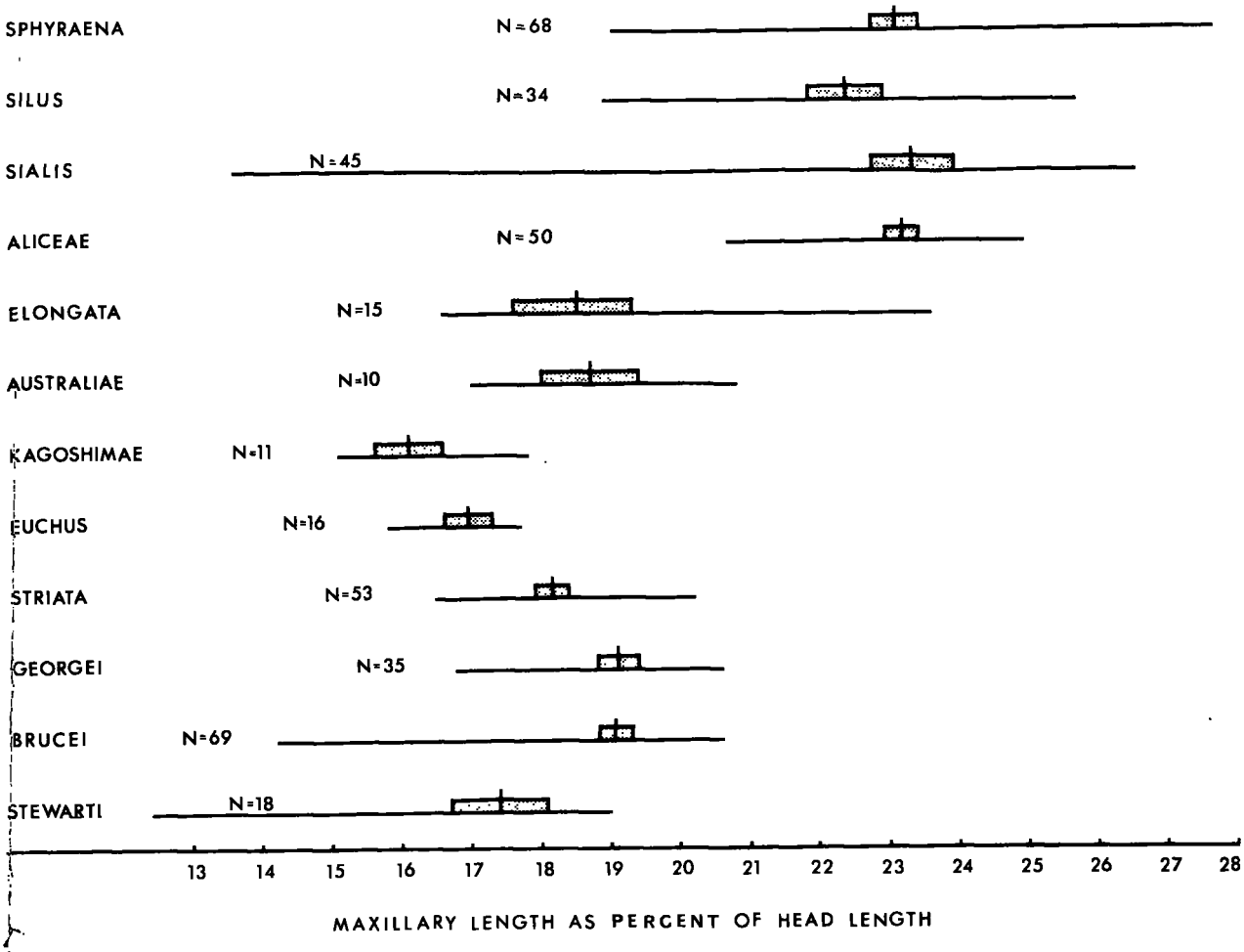

FIGURE 2.—Two species groups of *Argentina* as shown by maxillary length as percent of head length. Horizontal lines are ranges; bars are two standard errors on each side of means; vertical lines are means.

georgei and *brucei* have been taken together off Honduras (*Oregon* 3626) and at closely adjacent localities at similar depths off the south coast of Jamaica (*Oregon* 3549 and 3548). *A. georgei* and *stewarti* were caught in the same trawl off the Virgin Islands (*Oregon* sta. 2606). *A. striata* and *georgei* were caught at approximate localities and depths off the east coast of Florida, south of Dry Tortugas, and on the north coast of Cuba.

Figure 3 shows the distribution and figure 4 summarizes the co-occurrence of the four species. *A. brucei* and *georgei* each live with three other western Atlantic species; *striata* and *stewarti* each with two others. Only *A. striata* and *stewarti* are not so far known to co-occur.

We treat the four tropical western Atlantic forms as full species because they are sympatric, even though the magnitude of differences between them is less than the magnitude of differences separating species of the *silus* group. Although the western Pacific forms are not known to be sympatric, we recognize them also as full species. It is obvious that in the genus *Argentina*, characters of the magnitude of those separating *elongata*, *australiae*, and *kagoshimae* can signal the existence of full species.

SWIMBLADDER

The occurrence of silvery pigment in the outer layers of the swimbladded of some species of *Argentina* has been noted many times in the literature. Cohen (1958) added the observation that some species of *Argentina* lack this silvery pigment. He commented that presence or absence of silvery pigment did not seem to be a function of age, size, time of year, or method of preservation,

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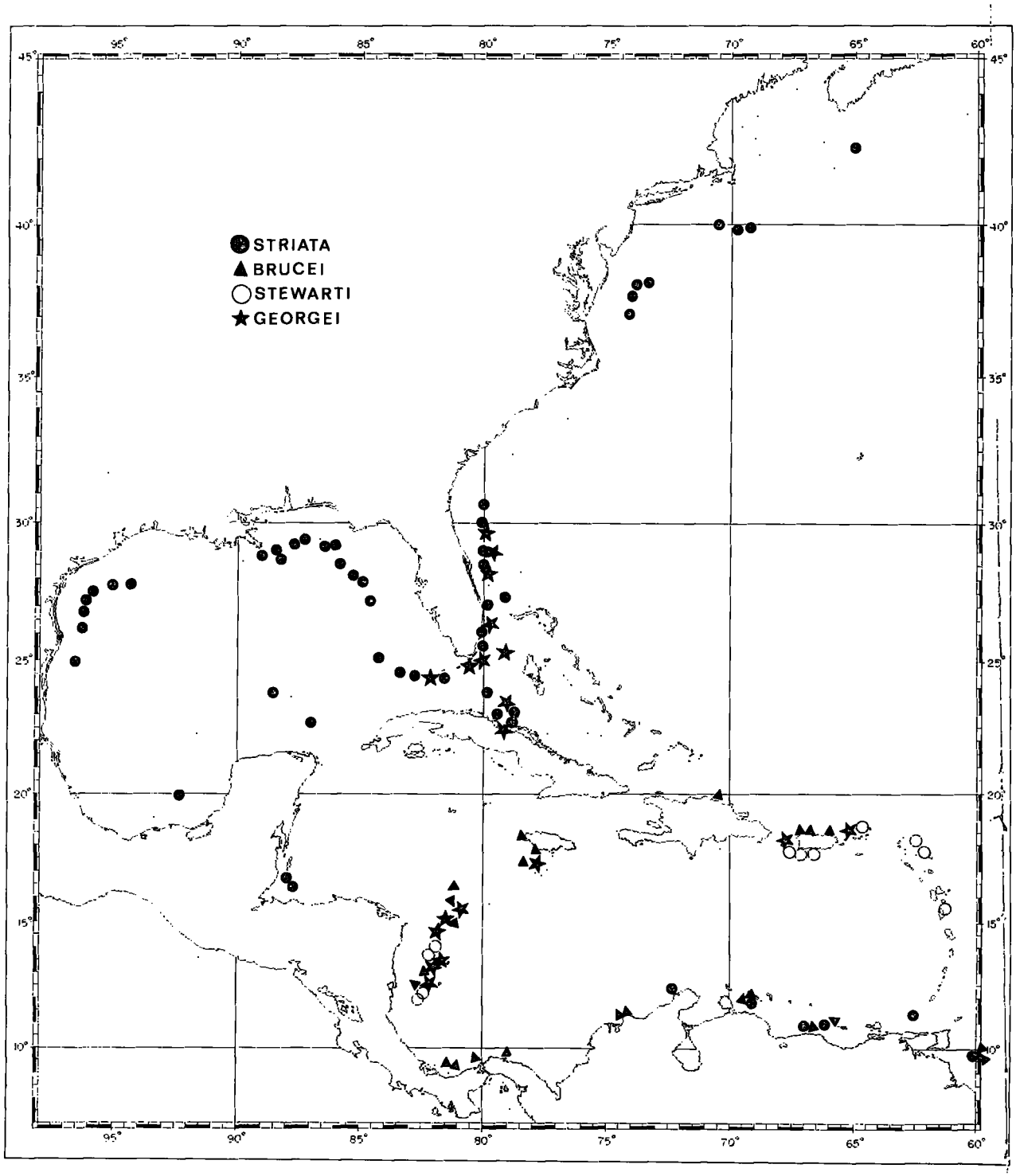

FIGURE 3.—Distribution of four species of *Argentina* in the western Atlantic.

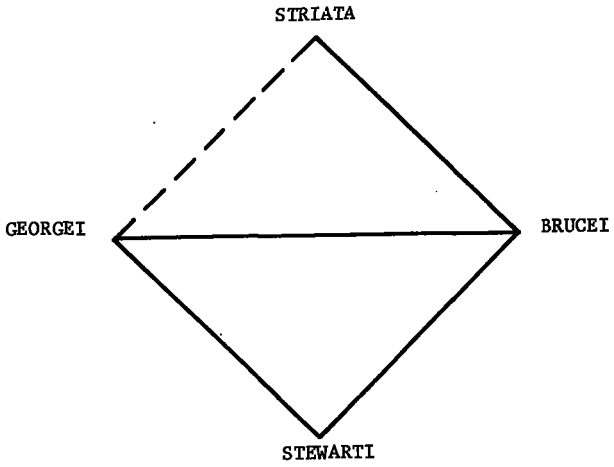

FIGURE 4.—Co-occurrence of four species of *Argentina* in the western Atlantic. Solid lines connect species taken from the same trawl. A dotted line connects species taken in different trawls at the same or closely adjacent localities.

and he, therefore, used the character taxonomically, although always in company with other characters. We here point out errors in Cohen's observations and comment on the variability of this character. In his key to the species of *Argentina* and in his diagnosis of *A. striata* Cohen stated that *A. striata* lacked a silvery-pigmented swimbladder. We have examined the swimbladders of 150 specimens of *A. striata* from throughout the range of the species and find that most, though not all of them, have definite silvery pigment. Cohen probably based his 1958 statement on examples of one or more of the other three species of *Argentina* from the western Atlantic.

The swimbladder of *A. striata* may have any one of four patterns of pigmentation. In one, the entire outer part of the organ is heavily coated with guanine (fig. 5); in the second, the anterior and posterior quarters of the bladders are pigmented with guanine, but the intervening segment lacks silvery pigment (fig. 5); in the third, only the posterior segment is pigmented with guanine; in the fourth and rarest type, the outer layer is faintly iridescent or appears to lack any impregnation of guanine.

In all but two instances, all specimens of *A. brucei* lack silvery pigment on the swimbladder (fig. 5). In a collection of six specimens from Venezuela (UF 5237), five individuals have iridescent to silvery pigment on each swimbladder, and a single individual lacks pigment completely. Also, one of three specimens from Honduras (FMNH 74571) has a silvery swimbladder.

All specimens examined of *A. stewarti* lack definite silvery pigment (fig. 5); however, one had a slightly iridescent swimbladder. A few examples of *A. georgei* have slightly iridescent swimbladders.

The specimens of *A. australiae*, *elongata*, and *kagoshimae* listed by Cohen (1958) were reexamined. The bladders were iridescent in *australiae;* pigment was lacking in the other two species.

The swimbladder pigmentation patterns discussed in this paper are valid only in preserved specimens.

Fänge (1958) has suggested that guanine might help to keep gases in the bladder. It would be interesting to test the diffusion rate of gases through the swimbladder walls of pigmented and unpigmented species of *Argentina.* In this respect we note that the small posterior chamber of the *Argentina* swimbladder, first described by Cohen (1958) and shown by Fahlén (1965) to have a resorbent function, invariably lacks silvery pigment.

According to Cohen (1958), argentinine fishes are physoclists that lack a rete mirabile. Such a condition is, of course, highly improbable unless there is some unknown method of gas being secreted into and maintained in the swimbladder. *Argentina* does in fact have a rete, which has been described for *A. silus* by Fänge (1958). He noted that it is a unique structure, different from the rete of other kinds of fishes. Marshall (1960) named it a micro-rete and described it in several other genera of argentinoid fishes.

KEY TO SPECIES OF *ARGENTINA*

1a. Branchiostegal rays 6, scales with spines ..... *2.*
1b. Branchiostegal rays 5, scales lacking spines ..... *3.*
2a. Lateral line scales 52 (50–54); gill rakers on lower arm of first arch 8 (7–10) ..... *A. sphyraena.*
2b. Lateral line scales 67 (64–69); gill rakers on lower arm of first arch 13 (11–17) .. *A. silus.*
3a. Gill rakers on lower arm of first arch 14–21; jaw relatively large, snout to maxillary tip distance usually less than 5 in head ..... *4.*

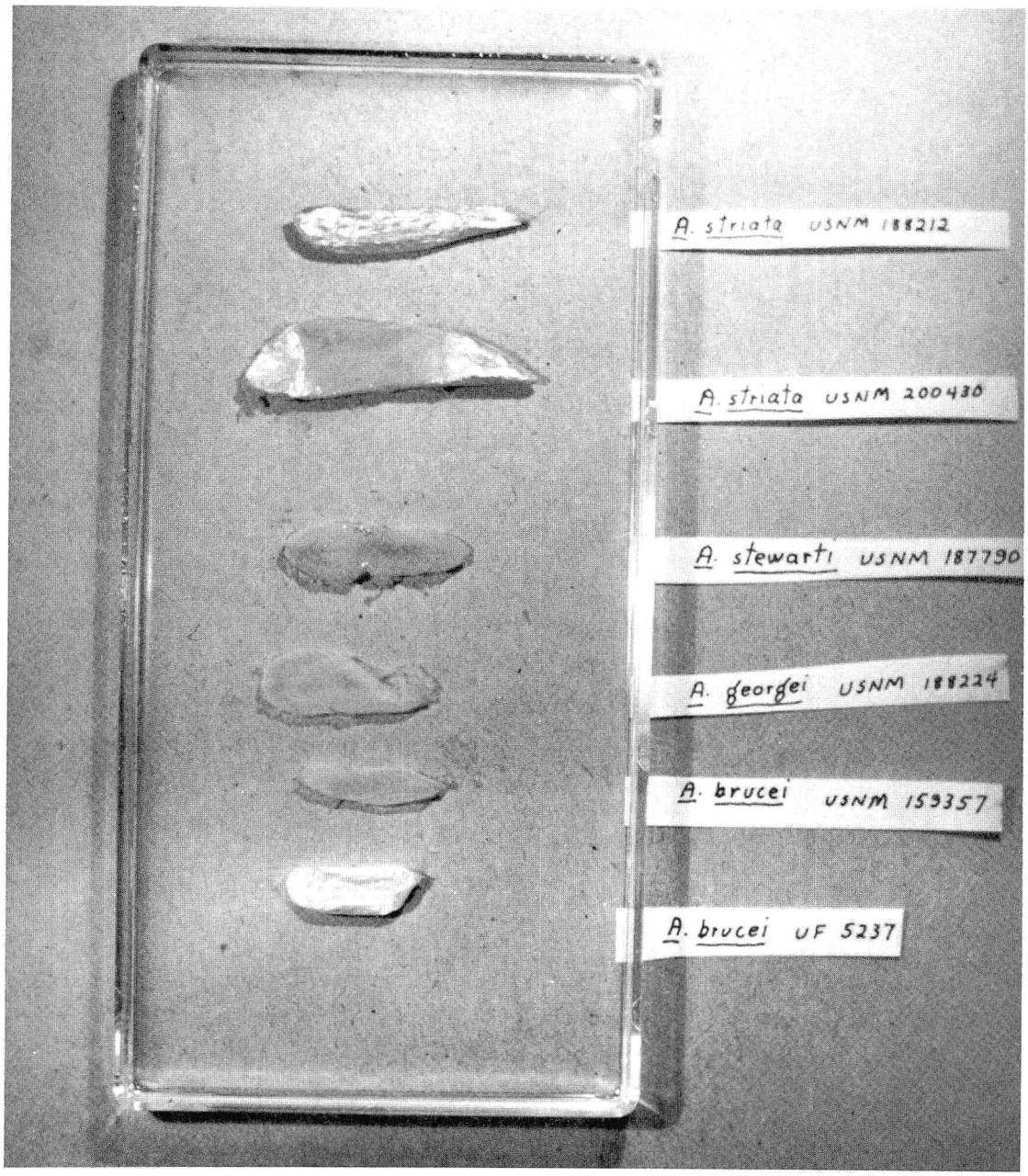

FIGURE 5.—Swimbladders from four species of western Atlantic *Argentina*. See text for explanation.

3b. Gill rakers on lower arm of first arch 5–10; jaw relatively small, snout to maxillary tip distance usually more than 5 in head ..... *5.*
4a. Head 3.0 (2.7–3.1) in standard length; eye 11.5 (10.5–12.7) in standard length; vertebrae 44 (43–45); lateral line scales 47 (45–48) ..... *A. aliceae* p. 19.
4b. Head 3.5 (3.2–3.7) in standard length; eye 14.3 (12.7–16.4) in standard length; vertebrae 48 (47–50); lateral line scales 49 (48–51) ..... *A. sialis* p. 22.
5a. Gill rakers on lower arm of first arch 9 (8–10) ..... *A. elongata.*
5b. Gill rakers on lower arm of first arch 5–7 ..... *6.*
6a. Pectoral fin rays 13–14 ..... *A. australiae.*

6b. Pectoral fin rays 15 or more ..... *7.*
7a. Ventral fin rays 10–12 ..... *8.*
7b. Ventral fin rays 12–15, usually 13 or more ..... *9.*
8a. Lateral line scale rows 54 (51–54); ventral fin rays 11–12, usually 12; anal fin rays 11–13, usually 12 or fewer; vertebrae 50–51 ..... *A. kagoshimae.*
8b. Lateral line scale rows 49 (47–50); ventral fin rays 10–11, usually 10; anal fin rays 13 or more; vertebrae 47–48 ..... *A. euchus* p. 33.
9a. Gill rakers on lower arm of first arch usually 7; vertebrae 45 (44–46) ..... *A. brucei* p. 31.
9b. Gill rakers on lower arm of first arch usually 6; vertebrae 47–54 ..... *10.*
10a. Swimbladder usually with definite silvery pigment or iridescence; pectoral fin rays 19 (18–21); body depth in standard length 8.2 (6.4–10.3); caudal peduncle depth in head length 5.2 (4.4–6.0); vertebrae 49 (47–51) ..... *A. striata* p. 22.
10b. Swimbladder lacking silvery pigment, sometimes iridescent; pectoral fin rays 17 (16–19); body depth in standard length 9.5 (7.4–12.0); caudal peduncle depth in head length 6.4 (5.6–7.3); vertebrae 48 (47–50) ..... *A. georgei* p. 27.
10c. Swimbladder lacking silvery pigment, sometimes iridescent; pectoral fin rays 20 (19–21); body depth in standard length 11.8 (9.1–13.6); caudal peduncle length in head length 6.0 (5.5–7.1); vertebrae 52–53 ..... *A. stewarti* p. 29.

ARGENTINA ALICEAE, NEW SPECIES

Figures 2, 6

Diagnosis

This species can be separated from *A. sphyraena* and *silus* by its smooth instead of spiny scales and by its five instead of six branchiostegals. *A. aliceae* differs from *sialis* in having a longer head, 33.7 (32.3–36.7) percent of standard length, in *sialis* 28.8 (27.3–31.2); a larger eye, 8.7 (7.9–9.5), in *sialis* 7.0 (6.1–7.9); fewer vertebrae, 44 (43–45), in *sialis* 48 (47–50); and fewer lateral line scales, 47 (45–48), in *sialis* 49 (48–51). It differs from all other species of *Argentina* in having 16 to 21 gill rakers on the lower arm of the first arch rather than 5 to 10.

Counts

See tables 1 to 7.

Measurements

Based on about 100 specimens, 83.2 to 143 mm. standard length, given as percent of standard length. Predorsal 48.6 (46.0–50.6); head length 33.7 (32.3–36.7); snout 10.5 (9.7–11.6); eye 8.7 (7.9–9.5); maxillary length 7.8 (7.0–9.1); depth at dorsal fin 17.3 (15.1–20.0); depth caudal peduncle 7.5 (6.9–8.7).

Description

Greatest depth at dorsal origin, tapering to caudal peduncle. Body in cross section deeper than wide; belly rounded. The head, when viewed laterally, has its dorsal profile slightly broken by the margin of the eye; the ventral profile rises to

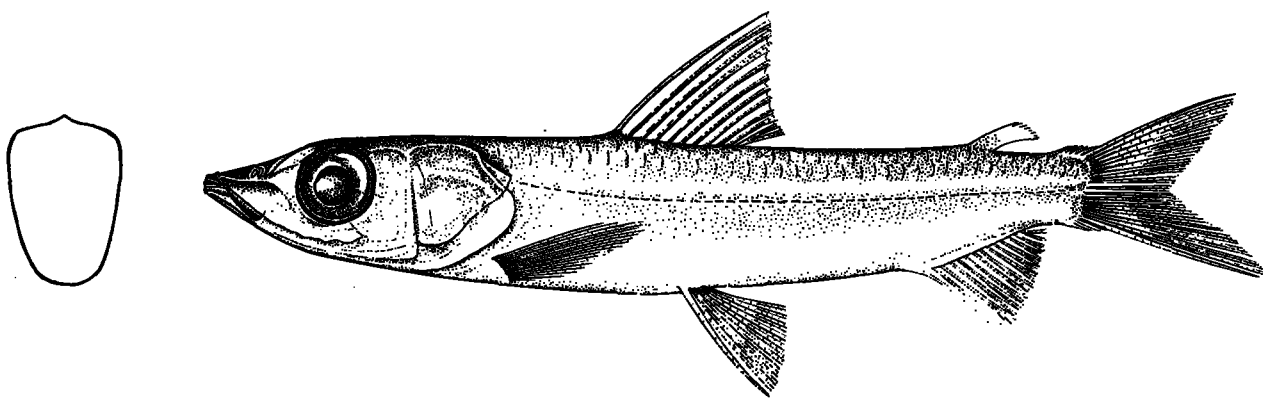

FIGURE 6.—*Argentina aliceae*, USNM 202462, holotype, 147 mm. standard length. All scales not shown. Cross section from in front of dorsal fin. Drawn by Mildred H. Carrington.

TABLE 1.—*Gill rakers on lower arm of first arch in species of* Argentina

Species	Gill rakers																
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
	Number of fish																
sphyraena			2	27	17	4											
silus							3	13	23	10	1						
sialis										1	2	9	22	6	4	1	
aliceae												1	8	29	13	3	1
elongata				5	13	12											
australiae		9	1														
kagoshimae	2	14															
euchus		17															
striata		76	2														
georgei		41	1														
brucei		1	87														
stewarti		21	1														

TABLE 2.—*Vertebral counts in species of* Argentina

Species	Number of vertebrae																
	43	44	45	46	47	48	49	50	51	52	53	54	—	64	65	66	67
	Number of fish																
sphyraena			1		1	3	1			1	5	4					
silus														2	2	2	1
sialis					4	67	13	1									
aliceae	1	47	27														
elongata									1	6	10	1					
australiae							2	2	3	1							
kagoshimae								2	5								
euchus					11	5											
striata					3	22	111	13	2								
georgei					4	31	8	4									
brucei		12	101	6													
stewarti										17	5						

TABLE 3.—*Dorsal fin ray counts in species of* Argentina

Species	Dorsal fin rays								
	9	10	11	12	13	14	15	16	17
	Number of fish								
sphyraena		12	46	3					
silus			2	32	23				
sialis			5	35	8				
aliceae			11	85	5				
elongata		3	12	4					
australiae		5	6	1					
kagoshimae		4	10	2					
euchus				15					
striata		1	39	18					
georgei		1	38	1					
brucei		1	67	5					
stewarti		1	14	6					

TABLE 4.—*Anal fin ray counts in species of* Argentina

Species	Anal fin rays								
	9	10	11	12	13	14	15	16	17
	Number of fish								
sphyraena			1	12	33	23	1		
silus					1	4	32	12	3
sialis					9	26	6		
aliceae					23	33	3		
elongata			4	5	7	4			
australiae				3	8				
kagoshimae			6	6	1				
euchus					9	5	1		
striata			3	20	34				
georgei		12	20	8	2				
brucei			9	36	27				
stewarti				11	10				

TABLE 5.—*Pectoral fin ray counts in species of* Argentina

Species	Pectoral fin rays										
	11	12	13	14	15	16	17	18	19	20	21
	Number of fish										
sphyraena		5	24	42	2						
silus					5	13	28	11			
sialis	5	35	8								
aliceae						1	20	14			
elongata			1	9	9	1					
australiae			8	3							
kagoshimae					6	9	2				
euchus						5	10	1			
striata								3	26	24	2
georgei						1	23	13	4		
brucei								30	30	4	
stewarti								1	7	8	6

TABLE 6.—*Ventral fin ray counts in species of* Argentina

Species	Ventral fin rays					
	10	11	12	13	14	15
	Number of fish					
sphyraena	6	49	6			
silus			44	13		
sialis	3	40	5			
aliceae	4	84	7			
elongata		13	6			
australiae		6	5	13		
kagoshimae		3	14			
euchus	14	2				
striata			4	9	40	3
georgei			4	22	8	
brucei				43	21	
stewarti				9	9	3

TABLE 7.—*Lateral line scales in three species of* Argentina

Species	Lateral line scales						
	45	46	47	48	49	50	51
	Number of fish						
sialis				7	20	18	1
aliceae	1	21	58	16			
euchus			1	4	11	1	

the snout in a gentle curve; the interorbital space between the supraocular canals is broadly concave. The frontals laterad to the canals arch upward slightly. The dorsal portion of the maxillary is hidden under the lacrimal and the jugal bones. The distal end of the maxillary is closer to the anterior margin of the eye than to the snout. Some specimens have a slight, bony knob at the symphysis of the lower jaw. The jaws are subequal; the upper broadly rounded, the lower less so. The palatine and the head of the vomer bear a continuous band 2 to 4 teeth wide composed of small, closely spaced, conical teeth; about 50 on the vomer and 25 to 30 on each palatine; dentary teeth are lacking. The ceratobranchial of the fifth gill arch bears 7 to 10 small, conical teeth; two patches of similar teeth, 5 to 10 on the anterior patch and 10 to 15 on the posterior patch, are found at the anterior end of the fourth suprabranchial. The tongue bears 6 strong recurved teeth (description of dentition based on a single alizarin-stained specimen). The gill rakers are elongate, compressed, and relatively widely spaced; the longest gill rakers are equal to about one-third of the interorbital distance.

The pectoral fin originates slightly ahead of a vertical through the posterior tip of the opercle. The anterior end of the pectoral fin base is elevated from the horizontal by an angle of 30 to 45 degrees. The distance between the bases of the innermost rays of the pectoral fins is less than the least depth of the caudal peduncle. The greatest height of the dorsal fin is usually greater than the maximum depth of the body. The greatest height of the anal fin is greater than the least depth of the caudal peduncle. The pectoral fins extend more than one-half the distance between the bases of the pectoral and ventral fins; the ventral fins are slightly shorter.

The scales lack spines. The lateral line scale count is summarized in table 7.

The peritoneum is colored with large, dark chromatophores, which are most densely distributed in the antero-dorsal section of the body cavity; the gut is immaculate. Ten to 14 pyloric caeca are present in 12 specimens. The body cavities of all specimens examined contained considerable amounts of fat.

The elongate swimbladder extends from about the level of the curve of the stomach to about the midlength of the ventral fin. The anterior tip of the swimbladder bears some silvery pigment, and the posterior one-third to one-half of the organ is strongly impregnated with silvery pigment.

Pigmentation in alcohol of adult specimens is light straw-colored on the lower two-thirds of the fish; the dorsum is darker; the muzzle is dusky, as are the nape and the upper portion of the opercle. Many specimens have the remnants of an iridescent band along the midline. In fishes less than about 95 mm. standard length, there is a series of 8 to 10 dusky blotches along the upper third of the body. In life the fish is a bright silvery color (H. A. Fehlmann, Smithsonian Oceanographic Sorting Center, personal communication).

Teratology

A single specimen from *Anton Bruun* sta. 640–B (USNM 202472) lacks pectoral fins. An X-ray photograph shows that a pectoral girdle is present.

Distribution

A. aliceae is known from nine localities along the northern coast of Peru, where it has been trawled at depths of 50 to 54 fm. (91–99 m.) to 105 to 170 fm. (192–311 m.); most specimens were taken between 55 and 88 fm. (100–161 m.).

Habits

This species has been taken only in bottom trawls and like most other *Argentina* apparently travels in schools a short distance above the bottom. The largest catch recorded was from *Anton Bruun* sta. 641–A, where 1,440 individuals weighing 44 kg. were taken. Several specimens examined had their stomachs tightly packed with partially digested crustaceans. Annotated station data from *Anton Bruun* cruise 16, which collected most of the study material, are presented by Chin (1966).

Name

Named for Alice Holland, former Secretary of this Laboratory, in recognition of her devoted services to ichthyology.

Study Material

All study material from Peru. Holotype: USNM 202462, 147 mm. standard length; R.V. *Anton Bruun* cruise 16, station 641–A, 6°54′ S., 80°44′ W., 97 to 110 m.; 6 June 1966; otter trawl. Paratypes: USNM 202459 (84 specimens, 1 cleared and stained); data as for holotype; from the same station MCZ (5); SIO (5). Paratypes: USNM 202460 (97); *Bruun* 640–B, 7°01′ S., 80°44′ W., 105 m.; otter trawl; from the same station USNM 202472 (1 lacking pectoral fins); FMNH (5); CAS (3). USNM 202463 (18); *Bruun* 639–A, 6°47′ S., 80°43′ W., 100 to 91 m.; otter trawl. USNM 202465 (1); *Bruun* 635–A, 6°27′ S., 80°56′ W., 160 m.; otter trawl. USNM 202464 (3); *Bruun* 631–A, 5°59′ S., 81°12′ W., 100 m.; otter trawl. USNM 202461 (320), *Bruun* 630–A, 6°02′ S., 81°12′ W., 160 m.; otter trawl; from the same station BMNH (5); UZMC (4); MNHN (3); ANSP (3). USNM 202466 (4); *Bruun* 627–A, 5°02′ S., 81°24′ W., 192 to 311 m.; otter trawl. USNM 202467 (2); *Bruun* 625–A, 4°57′ S., 81°23′ W., 118 to 133 m.; otter trawl. USNM 199802 (4); SW. of Lobos de Afuera Islands, Peru, 110 m.; trawl.

ARGENTINA SIALIS GILBERT

Figure 2

The heretofore northernmost locality for *A. sialis* is Monterey Bay, Calif. (Follett, 1945). An extension of the known range of about 1,120 km. is provided by a single specimen (147 mm. standard length) taken by the *John N. Cobb* off the coast of Oregon on 3 March 1962: USNM 188126, 46°04′ N., 124°39′ W., 100 to 102 fm. (183–187 m.), otter trawl, bottom temperature 8.3° C. The specimen agrees well with the description given by Cohen (1958).

Additional vertebral counts based on specimens from southern California listed by Cohen (1958) are presented in table 2.

ARGENTINA STRIATA GOODE AND BEAN

Figures 1, 2, 3, 4, 5, 7, 8, 9, 10A

Argentina striata Goode and Bean, 1896, p. 52, pl. 17, fig. 62 (original description; type-locality: *Albatross* station 2402, 28°36′ N. 85°33′ W., Gulf of Mexico, 111 fm. Holotype: USNM 43858, not designated in text of original description, but on p. 4 of the Atlas in the caption for pl. 17, fig. 62).

Diagnosis

This species can be separated from *A. sphyraena* and *silus* by its smooth instead of spiny scales and by its five instead of six branchiostegals. It differs from *silus*, *sialis*, *aliceae*, and *elongata* in having 6 (occasionally 7) gill rakers on the lower arm of the first arch, whereas the four species listed above have 8 to 21. It also differs in gill raker count from *A. brucei*, which has 7 (occasionally 6) rakers; also *striata* has 47 to 51 vertebrae; *brucei* has 44 to 46. It differs from *euchus* in having 12 to 15 ventral rays rather than 10 or 11. It differs from *kagoshimae*, *australiae*, *elongata*, *sialis*, and *sphyraena* in having 18 to 21 rather than 11 to 17 pectoral rays. It differs from *georgei* and *stewarti* in usually having silvery pigment on the swim-bladder, whereas the others lack it; from *stewarti* in having 47 to 51 vertebrae rather than 52 or 53; from *georgei* in having caudal peduncle depth in head length usually less than 5.7 rather than usually more than 5.7.

Counts

See tables 1 to 6.

Measurements

Based on about 55 specimens, 88.0 to 173 mm. standard length, given as percent of standard

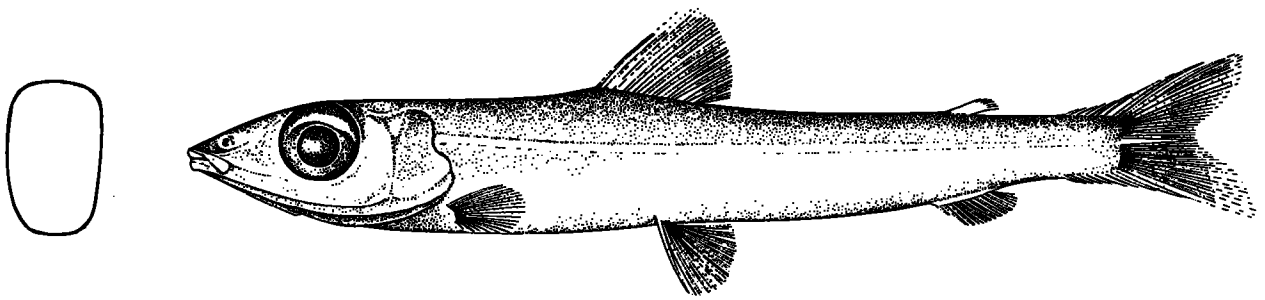

FIGURE 7.—*Argentina striata*, USNM 203003, 154 mm. standard length. Cross section from in front of dorsal fin. Scales not drawn. Drawn by Mildred H. Carrington.

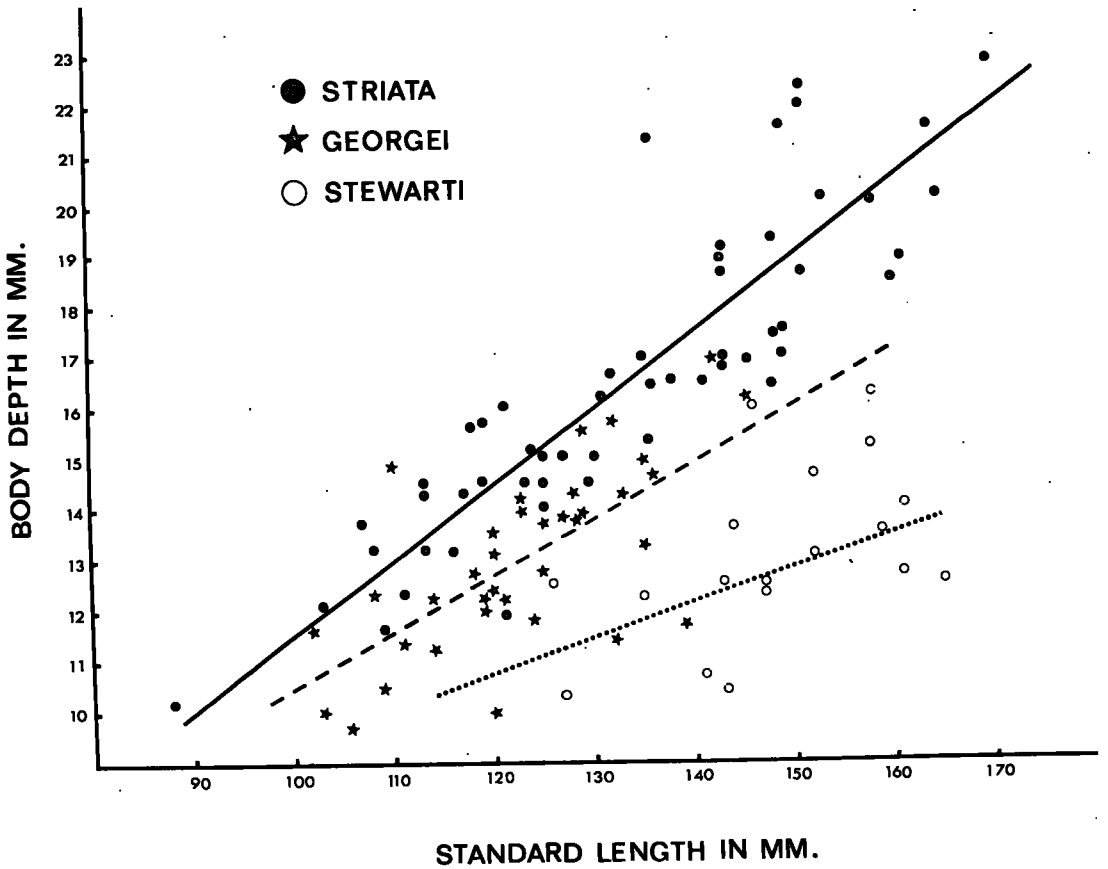

FIGURE 8.—Regressions of body depth (mm.) on standard length (mm.) for three closely related species of *Argentina*. See text for equations.

length. Preanal 83.5 (80.8–85.9); preventral 55.5 (52.2–58.0); predorsal 46.6 (44.2–48.6); head length 30.1 (26.1–32.0); snout 9.6 (8.5–10.6); eye 9.8 (7.8–10.9); maxillary length 5.4 (4.2–6.1); depth at dorsal fin 12.3 (9.7–15.7); depth caudal peduncle 5.8 (5.2–6.5).

Description

Body not very elongate. Greatest depth at dorsal origin, tapering to caudal peduncle. Figure 8 shows a regression of body depth on standard length ($Y=.150X-3.50$) compared with two closely related species. The caudal peduncle is also relatively deep. Figure 9 shows a regression of caudal peduncle depth on head length ($Y=.180X+.524$) compared with two closely related species. Body in cross section deeper than wide, dorsum and venter broadly rounded. The head, when viewed laterally, has its dorsal profile barely if at all broken by the upper margin of the eye; the ventral profile rises to the snout in a gentle curve; many specimens are preserved with the mouth open and the basibranchial projecting into the ventral profile. The interorbital space between the supraocular canals is flat or only slightly concave. The dorsal portion of the maxillary lies under the lachrymal. The distal end of the maxillary is usually about midway between the tip of the snout and the anterior margin of the eye. The jaws are broadly rounded, the lower slightly included. The palatine and the head of the vomer bear small, closely spaced, needlelike teeth in a continuous band from 2 to 5 teeth wide, about 30 on the vomer and 40 on each palatine; dentary teeth are lacking. The ceratobranchial of the fifth gill arch bears 9 small, conical teeth; two patches of similar teeth, 10 on the anterior patch and 14 on the posterior patch are at the anterior end of the fourth suprabranchial; there are also a few teeth on the third suprabranchial. The tongue bears eight strong recurved teeth (description of dentition based on a

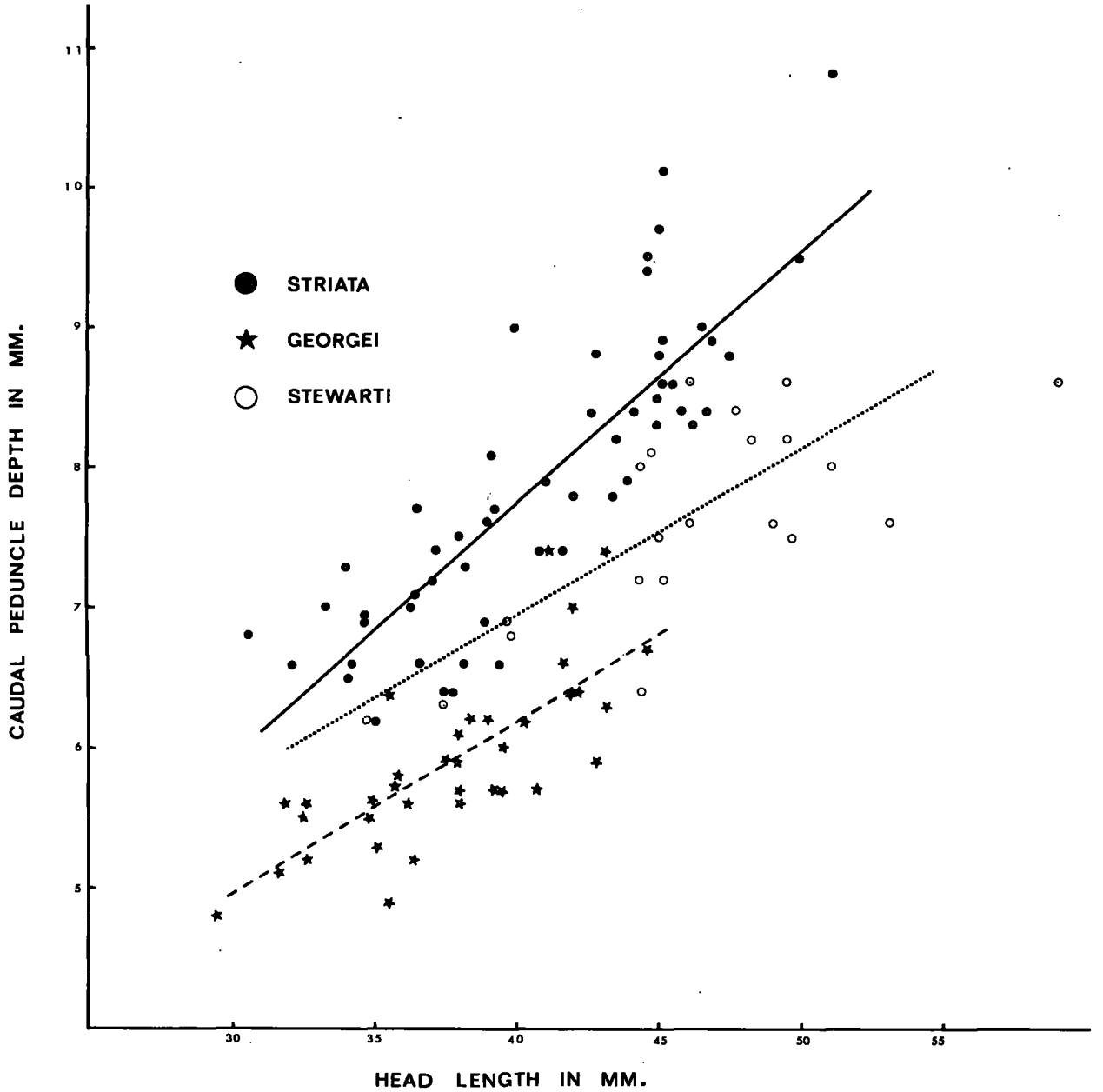

FIGURE 9.—Regressions of caudal peduncle depth (mm.) on head length (mm.) for three closely related species of *Argentina*. See text for equations.

single alizarin specimen). The gill rakers (fig. 1) are medium-sized, compressed, and widely spaced. The longest gill rakers are equal to one-fifth to one-sixth of the interorbital distance.

The pectoral fin originates close to the posterior margin of the opercle. The anterior end of the pectoral fin base is elevated from the horizontal by an angle of about 45 degrees; the distance between the innermost rays of the pectoral fins is about equal to or slightly less than the least depth of the caudal peduncle. In almost all of our specimens the pectoral and ventral fins are broken off short; however, in a few specimens, the pectorals appear to extend at least half the distance from the pectoral base to the ventral base. The ventral fins are probably shorter.

Scales and scale pockets are deciduous; however, the few scales we have seen lack spines. Lateral line counts of scale pockets in several specimens are about 50.

The peritoneum is black or almost so ventrally, grading to a less dense distribution of chromatophores laterally, then a darker band along the kidneys. The gut is immaculate. Nine to 14 pyloric caeca are present in 12 specimens. Most specimens have considerable fat in the body cavity. The swimbladder begins slightly anterior to the hind curve of the stomach and extends posteriorly to about the tip of the ventral fin. In 137 swimbladders examined, only 6 lacked any silvery pigment and several of these were iridescent. About one-half of the specimens having swimbladders that were completely impregnated with silvery guanine also had silvery pigment on the head, suggesting that strong formaldehyde solution that dissolves the silvery pigment on the body may also dissolve away pigment from the middle part of the swimbladder.

Pigmentation of adult specimens preserved in formaldehyde solution is variable, but in general the ventral two-thirds of the body is light. There is often a brown band above the lateral line; in some examples the band is barely discernible (fig. 7), in others quite distinct. Although the dark pigment of the peritoneum may show through the thin belly musculature, there is no externally pigmented band along the midventral line. Some specimens have the throat peppered with brown chromatophores (fig. 10A); in many, however, this region is immaculate. Specimens less than about 100 mm. standard length may have a row of eight or nine dusky blotches along the upper third of the body, but not all do. Alcohol-preserved specimens are silvery below the lateral line and on most of the head.

Distribution

A. striata is widely distributed in the western Atlantic, ranging from the offing of Nova Scotia (Schroeder, 1955), along the east coast of the United States, the north coast of Cuba, around the Gulf of Mexico, in the northwestern and southern Caribbean, and off the mouths of the Orinoco. There are two records, however, from much farther south off Brazil. Carvalho (1950) described specimens from Banco Sao Tomé at about lat. 22° S., and Miranda Ribeiro (1961) described and figured specimens from 24°14′ S., 44°49′ W. We have not examined material from either locality, but the descriptions fit our material of *A. striata*.

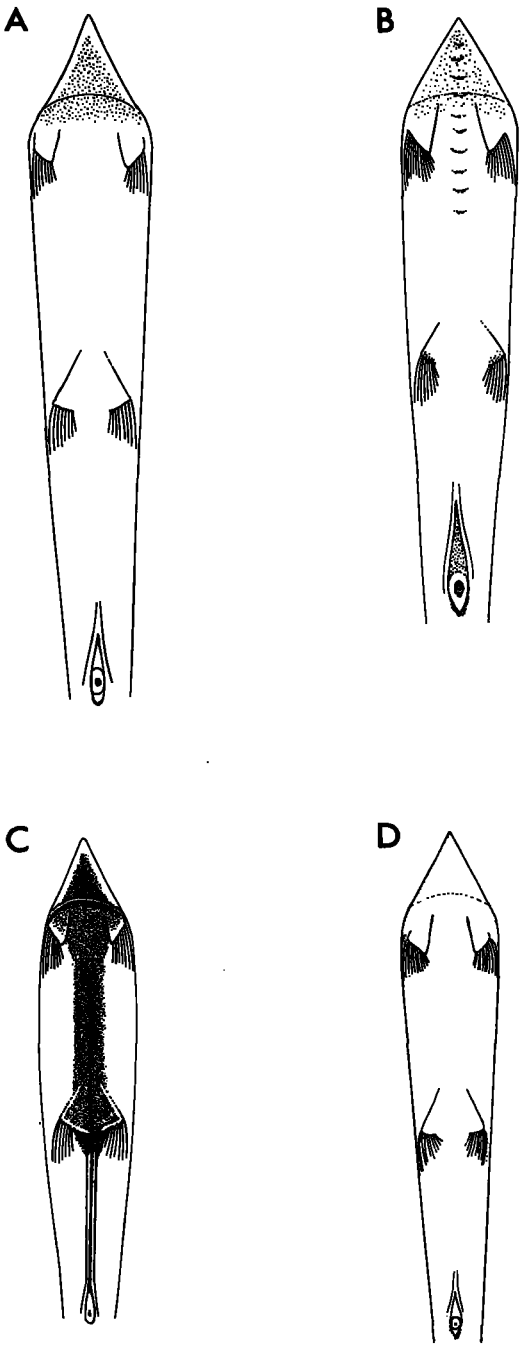

FIGURE 10.—Pigmentation on venters of four western Atlantic species of *Argentina:* A. *striata*, USNM 203001; B. *stewarti*, USNM 187834; C. *georgei*, USNM 186356; D. *brucei*, USNM 187793. Drawn by Mildred H. Carrington.

In the West Indies, *A. striata* has been taken only off the northern coast of Cuba and around the southern end of the Lesser Antilles; the records of *striata* given by Cohen (1958, 1964), Springer and Bullis (1956), and Bullis and Thompson (1965) from Hispaniola and the Lesser Antilles are of *striata*, *stewarti*, *georgei*, or *brucei*, or of combinations of these four.

Depth distribution ranges from 80 to 260 fm. (146–476 m.), but most records are from between 100 and 240 fm. (183–439 m.).

Habits

A. striata is taken with a bottom trawl, usually over a mud bottom at bottom temperatures ranging from 48° to 59° F. (8.9–15° C.). Specimens are caught singly and also in aggregations of as many as 100 individuals. Mixed collections of *A. striata* and *A. brucei* have been taken in the same haul.

Study Material

All from the Atlantic.

Bahama Banks.—MCZ 38476 (1 specimen), 22°45′ N., 78°45′ W., 150 to 180 fm. (274–329 m.). MCZ 40614 (1), 22°46′ N., 78°45′ W., 195 to 225 fm. (357–412 m.). UMML 11689 (10), 27°08′ N., 79°53′ W., 110 fm. (201 m.).

U.S. Atlantic.—UMML 12127 (21), 27°10′ N., 79°55′ W., 100 fm. (183 m.). MCZ 39817 (2), 27°17′ N., 79°49′ W., 200 fm. (366 m.). USNM 158082 (1), *Pelican* 25, 28°03′ N., 79°52′ W., 150 to 175 fm. (274–320 m.). TU 14774 (1), *Pelican* 60, 28° 29′ N., 79°54′ W., 160 to 190 fm. (293–348 m.). TABL 100559 (1), *Combat* 319, 28°31′ N., 79°52′ W., 180 fm. (329 m.). USNM 156659 (1), *Pelican* 204–4, 28°59′ N., 80°01.5′ W., 100 fm. (183 m.). USNM 188905 (1), *Oregon* 5094, 29°31′ N., 80°09′ W., 210 fm. (384 m.). TABL 100564 (11); *Silver Bay* 217, 29°41′ N., 80°08′ W., 180 to 200 fm. (329–366 m.). SU 49755 (1), 29°47′ N., 80°12′ W. TABL 100558 (1), *Silver Bay* 212, 29°59′ N., 80°07′ W., 200 fm. (366 m.). UMML 1461 (2) and UMML 529 (1), NE. coast of Florida, ESE. St. John's River Entrance, 105 fm. (192 m.). MCZ 38305 (4), 37°00′ N., 74°00′ W., 150 fm. (274 m.). MCZ 34568 (1), 37°36′ N., 74°17′ W., 100 fm. (183 m.). MCZ 38213 (9), 37°38′ N., 74°15′ W., 120 to 130 fm. (220–238 m.). USNM 186300 (1), *Delaware* 15–B, 37°42′ N., 74°12′ W., 150 to 225 fm. (274–412 m.). MCZ 39778 (6), 38°36′ N., 73°10′ W. MCZ 38341 (1), 38°38′ N., 73°10′ W., 190 to 200 fm. (348–366 m.). MCZ 37947 (1), 39°58′ N., 69°28′ W., 105 to 140 fm. (192–256 m.). MCZ 39973 (1), 39°59′ N., 69°35′ W, 82 to 85 fm. (150–155 m.). MCZ 37419 (1), *Captain Bill II* 35, 40°02′ N., 70°24′ W., 105 to 110 fm. (192–201 m.).

U.S. Gulf of Mexico.—UMML 16905 (1); 24°18′ N. 82°52′ W., 190 fm. (348 m.). UMML 16651 (1); 24°19′ N., 82°29′ W., 103 fm. (188 m.). TU 10901 (5); *Oregon* 1005, 24°20′ N., 83°20′ W., 190 fm. (348 m.). TU 12695 (12); *Oregon* 1548, 24°25′ N., 83°00′ W., 210 fm. (384 m.). TU 10917 (4); *Oregon* 1007, 24°26′ N., 83°24′ W., 180 fm. (329 m.). FMNH 66231 (1); *Oregon* 2671, 24°26′ N., 83°24′ W., 212 fm. (388 m.). FMNH 66230 (10); *Oregon* 2670, 24°27′ N., 83°26′ W., 210 fm. (384 m.). UMML 13289 (5); *Oregon* 4362, 24°30′ N., 83°33′ W., 190 fm. (348 m.). SU 49753 (1); *Oregon* 1009, 24°34′ N., 83°34′ W., 200 fm. (366 m.). SU 49726 (1); FMNH 59880 (19); *Oregon* 1026, 25°08′ N., 84°19′ W., 163 fm. (298 m.). TU 12669 (9); *Oregon* 1556, 26°24′ N., 98°45′ W., 210 fm. (384 m.). UMML 4441 (1); 28°07′ N., 85°13′ W., 150 fm. (274 m.). USNM 158687 (1); *Oregon* 953, 28°23′ N., 85°51′ W., 180 fm. (329 m.). SU 49724 (1); *Oregon* 1276, 28°30′ N., 86°11′ W., 240 fm. (439 m.). USNM 158686 (2); GCRL V60:119 (6); *Oregon* 36, 28°30′ N., 85°36′ W., 120 fm. (220 m.). USNM 43858, *holotype* and USNM 83864, *paratype* (1); *Albatross* 2402, 28°36′ N., 85°33′ W., 111 fm. (203 m.). FMNH 46270 (12); *Oregon* 277, 28°48′ N., 85°40′ W., 104 fm. (190 m.). TU 11698 (2); *Oregon* 1520–30, 29°00′ N., 88°00′ W., 200 to 250 fm. (366–457 m.). GCRL V62:731 (1); *Oregon* 3697, 29°00′ N., 88°36.5′ W., 190 to 200 fm. (348–366). USNM 203086 (1); *Oregon* 3725, 29°00.5′ N., 88°35.5′ W., 220 fm. (402 m.). USNM 156658 (2); *Pelican* 9, 29°02′ N., 88°41.5′ W., 120 to 169 1/2 fm. (220–310 m.). USNM 203087 (1); *Oregon* 3763, 29°03′ N., 88°34′ W., 190 fm. (348 m.). USNM 159349 (7); *Silver Bay* 156, 29°04′ N., 85°49′ W., 100 to 102 fm. (183–187 m.). USNM 188212 (18), TABL 100557 (2) and USNM 187836 (3); *Oregon* 3646, 29°07′ N., 88°34′ W., 125 fm. (229 m.). SU 49725 (1); *Oregon* 273, 29°09′ N., 85°59′ W., 110 fm. (201 m.). GCRL V63:933 (1); *Oregon* 60, 29°09′ N., 88°33′ W., 110 fm. (201 m.). GCRL V63: 932 (2); *Oregon* 32, 29°10′ N., 85°55′ W., 95 fm. (174 m.). USNM 188387 (1); GCRL V62: 730 (1); *Oregon* 3676,

29°10′ N., 88°10′ W., 200 fm. (366 m.). UMML 1508 (1); 29°10′ N., 88°20′ W., 150 fm. (274 m.). USNM 188389 (3); *Oregon* 3677, 29°11′ N., 88°06′ W., 200 fm. (366 m.). USNM 158127 (1); SU 49727 (1); *Oregon* 1246, 29°15′ N., 88°11′ W., 200 to 210 fm. (366–384 m.). SU 17441 (1); 29°15.5′ N., 87°53′ W. FMNH 45932 (2); *Oregon* 864, 29°19′ N., 86°04′ W., 82 fm. (150 m.). FMNH 46269 (5); *Oregon* 265, 29°20′ N., 87°42′ W., 101 fm. (185 m.). USNM 159013 (1); *Oregon* 1260, 29°23′ N., 86°48′ W., 250 fm. (457 m.). SU 49723 (1) and FMNH 46268 (2); *Oregon* 269, 29°27.5′ N., 87°26.5′ W., 150 fm. (274 m.). USNM 158842 (1); *Oregon* 1400, 29°30′ N., 87°08′ W., 210 fm. (384 m.). TU 11761 (2); *Oregon* 946, 29°41′ N., 86°44′ W., 100 fm. (183 m.). TU 2716 (7); *Oregon* 278, 29°49′ N., 85°45′ W., 112 fm. (205 m.).

Mexico.—SU 49721 (1); *Oregon* 1054, 19°37′ N., 92°40′ W., 200 fm. (366 m.). FMNH 45728 (1); *Oregon* 726, 22°41.9′ N., 86°41.2′ W., 225 fm. (412 m.). USNM 186068 (2); *Silver Bay* 1184, 23°56′ N., 87°32′ W., 150 fm. (274 m.). TU 12939 (7); UF 1316 (2); *Oregon* 1091, 26°46′ N., 96°20′ W., 200 to 210 fm. (366–384 m.). FMNH 46266 (2); *Oregon* 550, 26°55′ N., 96°25.5′ W., 125 fm. (229 m.). TU 10998 (4); *Oregon* 1094, 27°10′N., 96°20′ W., 150 fm. (274 m.). FMNH 45050 (1); 27°15′ N., 96°15′ W., 200 fm. (366 m.). TU 2770 (4); *Oregon* 164, 27°21′ N., 96°06′ W., 160 fm. (293 m.). USNM 203000 (1); *Oregon* 4617, 27°48′ N., 94°37′ W., 200 fm. (366 m.).

Central America.—USNM 187835 (1); *Oregon* 3634, 16°44′ N., 87°55′ W., 190 fm. (348 m.).

South America.—UF 8026 (2); FMNH 66223 (11); *Oregon* 1989, 9°45′ N., 59°45′ W. USNM 203046 (1); *Oregon* 4465, 10°45′ N., 66°37′ W., 125 fm. (229 m.). USNM 203003 (5); *Albatross* 2700, 10°59′ N., 66°00′ W., 140 fm. (256 m.). TABL 100556 (4); *Oregon* 5037, 11°36′ N., 62°46′ W., 200 to 240 fm. (366–439 m.). USNM 203002 (1); *Oregon* 4410, 11°52′ N., 69°27′ W., 230 fm. (421 m.). USNM 200430 (1); *Oregon* 5690, 12°30′ N., 72°08′ W., 257 fm. (470 m.).

Antilles.—MCZ 40617 (1); *Albatross* 3422, 22°48′ N., 79°09′ W., 235 fm. (430 m.). MCZ 40010 (1); 22°49′ N., 79°07′ W., 235 fm. (430 m.). MCZ 40618 (1); 22°52′ N., 79°22′ W., 240 fm. (439 m.).

ARGENTINA GEORGEI, NEW SPECIES

Figures 2, 3, 4, 5, 8, 9, 10C, 11

Diagnosis

This species can be separated from *A. sphyraena* and *silus* by its smooth instead of spiny scales and by its five rather than six branchiostegals. It differs from *silus*, *sialis*, *aliceae*, and *elongata* in having 6 (occasionally 7) gill rakers on the lower arm of the first arch—the four species listed above have 8 to 21. It differs in gill raker count from *A. brucei*, which has 7 (occasionally 6) rakers; also *georgei* has 47 to 50 vertebrae, *brucei* has 44 to 46. It differs from *euchus* in having 12 to 14 ventral rays rather than 10 or 11. It differs from *sphyraena*, *sialis*, *elongata*, and *australiae* in having 16 to 19 pectoral rays rather than 11 to 16. It differs from *kagoshimae* in having vertebrae usually less than 50 rather than usually more than 50; pectoral rays 16 to 19 rather than usually less than 17; ventral rays usually 13 or 14 rather than 11 or 12. It differs from *striata* in lacking silvery pigment on the swimbladder; in having anal rays usually 10 or 11 rather than 12 or 13, pectoral rays usually 17 or 18 rather than 19 or 20, and caudal peduncle depth in head length usually more than 6 rather than 6 or less. It differs from *stewarti* in having 47 to 50 vertebrae rather than 52 or 53, in

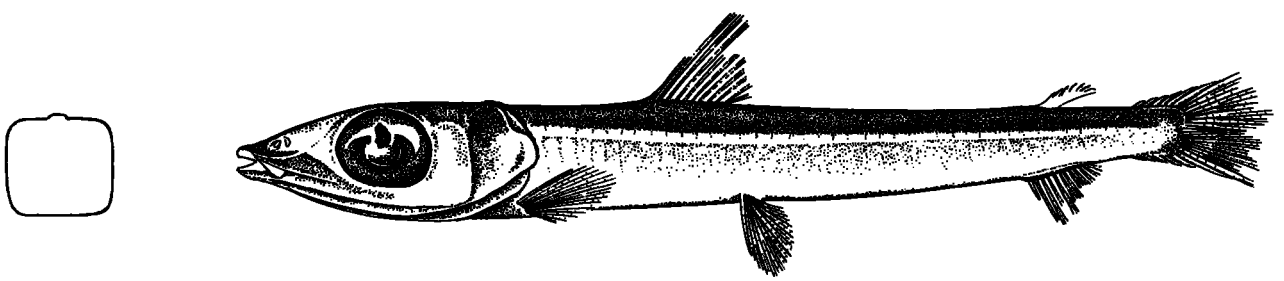

FIGURE 11.—*Argentina georgei*, USNM 188224, paratype, 109 mm. standard length. Scales not shown. Cross section from in front of dorsal fin. Drawn by Mildred H. Carrington.

having usually 10 or 11 anal rays rather than 12 or 13, and in having pectoral rays usually 17 or 18 rather than 19 to 21.

Counts

See tables 1 to 6.

Measurements

Based on 37 specimens, 102 to 146 mm. standard length given as percent of standard length. Preanal 85.1 (83.3–86.3); preventral 55.6 (53.7–58.6); predorsal 46.4 (44.9–48.6); head length 30.6 (28.5–32.4); snout 10.0 (8.7–11.2); eye 9.4 (8.2–10.9); maxillary length 5.8 (5.2–6.6); depth at dorsal fin 10.6 (8.3–13.4); depth caudal peduncle 4.8 (4.3–5.6).

Description

Body of medium length. Figure 8 shows a regression of body depth on standard length ($Y=.120X-.504$) compared with two closely related species. Greatest depth behind head, tapering to the relatively narrow caudal peduncle. Figure 9 shows a regression of caudal peduncle depth on head length ($Y=.123X+1.28$) compared with two closely related species. Body in front of dorsal fin almost square in cross section or somewhat wider than deep; compressed posteriorly. Dorsum and venter flat, not rounded. The head, when viewed laterally, as deep or deeper than the body, its dorsal profile barely or not at all broken by the upper margin of the eye; the dorsal and ventral profiles of the head converge at about equal angles on the snout. The interorbital space between the supraocular canals is broadly concave. The dorsal portion of the maxillary lies under the lachrymal. The distal end of the maxillary reaches to at least the midpoint of the distance from the tip of the snout to the anterior margin of the orbit and usually farther. The jaws are broadly rounded, the lower included; there is a slight, bony protuberance behind the symphysis of the lower jaw. The palatine and the head of the vomer bear small, closely spaced, needlelike teeth in a continuous band 2 to 5 teeth wide, about 40 on the vomer and 50 on each palatine; no dentary teeth. The ceratobranchial of the fifth gill arch bears 8 small, conical teeth; two patches of similar teeth, 5 on the anterior patch and 15 on the posterior patch, are at the anterior end of the fourth suprabranchial. The third suprabranchial lacks teeth. The tongue bears eight strong, recurved teeth (description of dentition based on a single alizarin-stained specimen). The gill rakers are medium-sized, compressed, and widely spaced. The longest rakers equal one-seventh to one-eighth of the interorbital distance.

The pectoral fin originates on the ventral surface of the fish anterior to a vertical through the rear margin of the opercle; the distance between the innermost rays of the pectoral fins is equal to or, more often, greater than the least depth of the caudal peduncle. The fin rays of all specimens are broken off short.

Scales deciduous, the few we have seen lack spines. Lateral counts of scale pockets in several specimens are about 50.

The peritoneum is dark. The gut is immaculate. Eight or nine pyloric caeca are present in eight specimens. The swimbladder begins close to the hind curve of the stomach and extends posteriorly to slightly beyond the origin of the ventral fin. Swimbladder lacking silvery pigment (fig. 5), however, we have seen several specimens with slightly iridescent bladders.

Pigmentation of adult specimens preserved in formaldehyde is distinctive and consists of a dark brown band extending along the upper quarter of the side; it is not continuous over the dorsum; however, there is a dark, middorsal streak. The venter and throat of most specimens are pigmented with large, dark chromatophores which form a wide dark band extending to the pelvics (fig. 10C), and in many specimens all the way to the vent. In some specimens the superficial pigmentation of the belly is poorly developed, and in these the darkly pigmented peritoneum shows through the thin ventral musculature.

Distribution

A. georgei is found off the east coast of Florida and barely enters the Gulf of Mexico south of Dry Tortugas. It has also been taken at several localities along the western side of the Bahama Banks and on the north coast of Cuba. In the Caribbean and along the Antilles, *A. georgei* has been trawled off Honduras, Nicaragua, and Jamaica and near Puerto Rico and the Virgin Islands (fig. 4).

Depth distribution ranges from 120 to 250 fm. (220–457 m.), but the fish has been most often caught between 150 and 220 fm. (274–402 m.).

Habits

A. georgei has been taken only in bottom trawls over mud and shell bottoms at bottom tempera-

tures of 48, 58, 61, and 62° F. (8.9, 14.4, 16.1, and 16.7° C.). Specimens are most often taken singly. Our largest sample has six individuals. *A. georgei* has been taken with *brucei* and with *stewarti*.

Name

Named for George Clipper, to whom we are indebted for efficient assistance in this Laboratory.

Study Material

All from the Atlantic. Holotype: USNM 203016, 125 mm. standard length, *Oregon* 3622, 16°01′ N., 81°08′ W., 145 to 150 fm. (265–274 m.), June 6, 1962. Paratypes:

Bahama Banks.—FMNH 65791 (1 specimen), *Oregon* 1343, 22°59′ N., 79°17′ W., 250 fm. (457 m.). TABL 100575 (1), *Silver Bay* 2457, 23°43′ N., 79°07′ W., 250 fm. (457 m.). FMNH 66217, *Combat* 446, 25°10′ N., 79°13′ W., 250 fm. (457 m.). UF 1350 (1), *Combat* 235, 27°27′ N., 78°58′ W., 180 fm. (329 m.). USNM 158689 (1), *Combat* 237, 27°28′ N., 78°44′ W., 215 fm. (393 m.).

U.S. Atlantic.—TABL 100563 (4), *Combat* 441, 25°16′ N., 80°00′ W., 185 fm. (338 m.). TABL 100569 (1), *Silver Bay* 2482, 26°07′ N., 79°12′ W., 200 fm. (366 m.). TABL 100567 (1), *Silver Bay* 218, 29°38′ N., 80°11′ W., 220 fm. (402 m.). TABL 100573 (5), *Combat* 491, 29°30′ N., 80°10′ W., 125 fm. (229 m.).

U.S. Gulf of Mexico.—UMML 2882 and 2545 (1 each); *Combat* 281, 24°17′ N., 82°47′ W., 215 fm. (393 m.).

Central America.—USNM 187841 (5), *Oregon* 3579, 12°26′ N., 82°26′ W., 125 fm. (229 m.). USNM 203017 (4) and MCZ (2), *Oregon* 6423, 13°28′ N., 82°01′ W., 150 to 158 fm. (274–289 m.). USNM 187839 (6), *Oregon* 3566, 14°10′ N., 81°58′ W., 150 to 160 fm. (274–293 m.). USNM 188224 (4), *Oregon* 3622, data as for holotype. USNM 187834 (3, 1 cleared and stained), *Oregon* 3625, 16°26′ N., 81°35′ W., 120 fm. (220 m.). ANSP 98604 (4), *Oregon* 3626, 16°45′ N., 81°27′ W., 150 fm. (274 m.).

Antilles.—USNM 187816 (2); *Oregon* 3548, 17°53′ N., 77°56′ W., 150 fm. (274 m.). TABL 100572 (3); *Silver Bay* 5193, 18°16′ N., 67°22′ W., 150 fm. (274 m.). FMNH 66224 (1); *Oregon* 2606, 18°37.5′ N., 65°04′ W., 210 fm. (384 m.). USNM 157980 (1); *Oregon* 1344, 22°50′ N., 79°08′ W., 200 to 225 fm. (366–412 m.). USNM 157976 (1); *Oregon* 1343, 22°59′ N., 79°17′ W., 250 fm. (457 m.).

ARGENTINA STEWARTI, NEW SPECIES

Figures 2, 3, 4, 5, 8, 9, 10B, 12

Diagnosis

This species can be separated from *A. sphyraena* and *silus* by its smooth instead of spiny scales and by its five instead of six branchiostegal rays. It differs from *silus*, *sialis*, *aliceae*, and *elongata* in having 6 (occasionally 7) gill rakers on the lower arm of the first arch—the four species listed above have 8 to 21. It differs in gill raker count from *A. brucei* which has 7 (occasionally 6) rakers. *A. stewarti* differs from *sialis*, *aliceae*, *kagoshimae*, *euchus*, *striata*, *georgei*, and *brucei* in having 52 or 53 vertebrae—the others have 43 to 51. It differs from *sphyraena*, *sialis*, *elongata*, *australiae*, and *kagoshimae* in having 18 to 21 pectoral rays rather than 11 to 17. It differs from *sphyraena*, *sialis*, *aliceae*, *elongata*, *kagoshimae*, and *euchus* in having 13 to 15 ventral rays rather than 10 to 12. It differs from *striata* in lacking silvery pigment on the swimbladder (occasionally lacking in *striata*) and in its more slender body, depth usually 10 or more times in standard length rather than usually less than 9 in standard length in *striata*. It differs from *georgei* in having anal rays 12 or 13 rather than usually 10 or 11 and in having pectoral rays usually 19 or more, rather than usually 18 or fewer.

Counts

See tables 1 to 6.

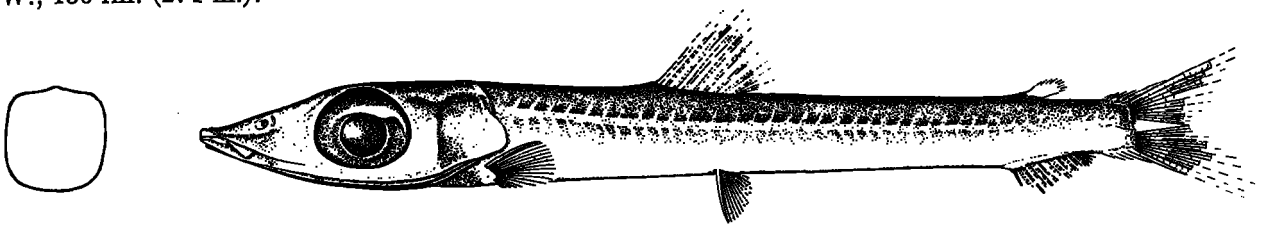

FIGURE 12.—*Argentina stewarti*, USNM 202998, paratype, 148 mm. standard length. Scales not shown. Cross section from in front of dorsal fin. Drawn by Mildred H. Carrington.

Measurements

Based on 18 specimens, 121 to 166 mm. standard length, given as percent of standard length. Preanal 85.0 (83.5–86.7); preventral 55.8 (53.8–57.3); predorsal 47.7 (46.4–49.1); head length 30.6 (28.8–33.0); snout 10.3 (10.1–10.5); eye 9.7 (8.7–10.7); maxillary length 5.3 (3.8–5.9); depth at dorsal fin 8.6 (7.3–11.0); depth caudal peduncle 5.1 (4.5–5.5).

Description

Body elongate. Figure 8 shows a regression of body depth on standard length (Y=.069X+2.43) compared with two closely related species. Greatest depth behind head, tapering little to the caudal peduncle. Figure 9 shows a regression of caudal peduncle depth on head length (Y=.112X+2.44) compared with two closely related species. Body in cross section in front of dorsal fin usually wider than deep, approximately rectangular. The head, when viewed laterally, has its dorsal profile slightly interrupted by the upper margin of the eye; the ventral profile of the head rises gently to the snout. The interorbital space between the supraocular canals flat or barely concave. The dorsal portion of the maxillary lies under the lachrymal. The distal end of the maxillary is midway between the tip of the snout and the anterior margin of the orbit. The jaws are broadly rounded, the lower included. The palatine and the head of the vomer bear small, closely spaced, needlelike teeth in a continuous band 2 to 5 teeth wide, about 30 on the vomer and 45 on each palatine; no dentary teeth. The ceratobranchial of the fifth gill arch bears 14 small, conical teeth; two patches of similar teeth, with about 18 on each are found at the anterior end of the fourth suprabranchial. The tongue bears eight strong recurved teeth (description of dentition based on a single alizarin specimen). The gill rakers are widely spaced triangular flaps; the longest ones are equal to one-seventh to one-eighth of the interorbital distance.

The pectoral fin originates on the ventral surface of the body anterior to a line through the hind margin of the opercle. The distance between the inner rays of the pectoral fins is equal to or greater than the least depth of the caudal peduncle. The rays of all fins are broken off short.

Scales deciduous; the few we have seen lack spines. Lateral scale pockets about 55.

The peritoneum is densely punctulate with small dark chromatophores. Several specimens have the gut lightly peppered with chromatophores. Seven to nine pyloric caeca are present in eight specimens. The swimbladder begins close to the hind curve of the stomach and extends posteriorly to beyond the origin of the ventral fin. Swimbladder lacking silvery pigment (fig. 5); however, we have seen one specimen with an iridescent swimbladder.

Pigmentation of adult specimens preserved in formaldehyde solution consists of a dark brown band extending along the upper one-fourth of the body; ventral and parallel to the band is a less darkly pigmented area. These two pigment bands color the entire upper one-half of the body. The dorsum is unpigmented with the exception of a narrow middorsal streak. The throat and breast are peppered with chromatophores, which in some specimens are also scattered at the bases of the ventral fins (fig. 10B). In some specimens the peritoneum shows through the belly as a dark, midventral streak. Some specimens also have some of the scale pockets of the venter outlined in dark pigment.

Distribution

A. stewarti has been taken off Nicaragua in the western Caribbean and from Mona Island to Dominica in the Antilles (fig. 4). It seems likely that it is widespread in the southern Caribbean.

Depth distribution ranges from 200 to 310 fm. (366–567 m.)—deeper than the other three Gulf and Caribbean species. *A. stewarti* does overlap the lower half of the depth distributions of the other three; however, it is the only species that has not been taken shoaler than 200 fm. (366 m.).

Habits

We have little information on this species. It has been taken only with a bottom trawl; however, we have no information on bottom type or temperature. Specimens are most often taken singly; however, we have one collection with six fishes. *A. stewarti* has been taken with *georgei* and *brucei*.

Name

Named for Stewart Springer in recognition of his numerous contributions to the ichthyology of the tropical western Atlantic.

Study Material

All from the Atlantic. Holotype; USNM 202996, 144 mm. standard length; *Oregon* 3565, 14°10′ N.,

81°55′ W., 240 to 250 fm. (439–457 m.), May 21, 1962. Paratypes:

Central America.—USNM 203572 (1 specimen); *Oregon* 3610, 12°23′ N., 82°29′ W., 200 fm. (366 m.). USNM 202998 (4); *Oregon* 3574, 12°31′ N., 82°21′ W., 200 fm. (366 m.). USNM 188223 (1); *Oregon* 3614, 14°00′ N., 81°50′ W., 200 fm. (366 m.). USNM 202997 (1); USNM 187790 (6); *Oregon* 3565, data as for holotype.

Antilles.—MCZ (1); *Oregon* 5925, 15°38′ N., 61°15′ W., 245 fm. (448 m.). FMNH 66225 (1); *Oregon* 2636, 17°37′ N., 63°36′ W., 280 fm. (512 m.). USNM 202999 (2, 1 cleared and stained); *Oregon* 6695, 17°41′ N., 62°50.5′ W., 300 to 320 fm. (549–585 m.). USNM 186356 (1); *Oregon* 2645, 18°12′ N., 67°42′ W., 260 fm. (476 m.). FMNH 66226 (1); *Oregon* 2651, 18°16.5′ N., 67°17′ W., 250 fm. (457 m.). USNM 108374 (1); *Caroline*, 18°32′ N., 68°21′ W., 260 fm. (476 m.). FMNH 66224 (2); *Oregon* 2606, 18°37.5′ N., 65°04′ W., 210 fm. (384 m.).

ARGENTINA BRUCEI, NEW SPECIES

Figures 2, 3, 4, 5, 8, 9, 10D, 13

Argentina striata not of Goode and Bean, 1896; Cohen, 1964 (fig. 5).

Diagnosis

A. brucei differs from *sphyraena* and *silus* in having smooth instead of spiny scales and five instead of six branchiostegal rays. It differs from *silus*, *sialis*, *aliceae*, and *elongata* in having seven (sometimes six) gill rakers on the lower arm of the first arch rather than eight or more. It differs from all *Argentina* except *sphyraena* and *aliceae* in its low vertebral count, 44 to 46 rather than 47 or more. It differs from *sphyraena*, *sialis*, *elongata*, *australiae*, and *kagoshimae* in having 18 to 20 pectoral rays rather than 19 or fewer. It differs from *elongata*, *kagoshimae*, and *euchus* in having 13 or 14 ventral rays rather than 12 or fewer. It differs from *australiae*, *kagoshimae*, *euchus*, *striata*, *georgei*, and *stewarti* in having usually seven gill rakers rather than usually six gill rakers. It differs from *striata* in usually lacking silvery pigment on the swimbladder.

Counts

See tables 1 to 6.

Measurements

Based on about 72 specimens, 68.4 to 132 mm. standard length, given as percent of standard length: Preanal 84.5 (74.6–87.9); preventral 56.2 (52.9–58.8); predorsal 48.3 (44.4–50.7); head length 31.2 (27.7–33.1); snout 10.1 (8.7–11.2); eye 10.0 (7.9–11.6); maxillary length 5.9 (4.6–6.6); depth at dorsal fin 13.0 (10.9–15.4); depth at caudal peduncle 5.9 (5.0–6.5).

Description

A relatively short-bodied species with greatest depth at dorsal origin tapering to caudal peduncle. Body in cross section deeper than wide, the venter broadly rounded. Body in preserved specimens notably soft. The head, when viewed laterally, usually has its dorsal profile broken by the upper margin of the eye. The dorsal and ventral profiles of the head converge on the snout at about equal angles. The interorbital space between the supraocular canals is flat. The dorsal portion of the

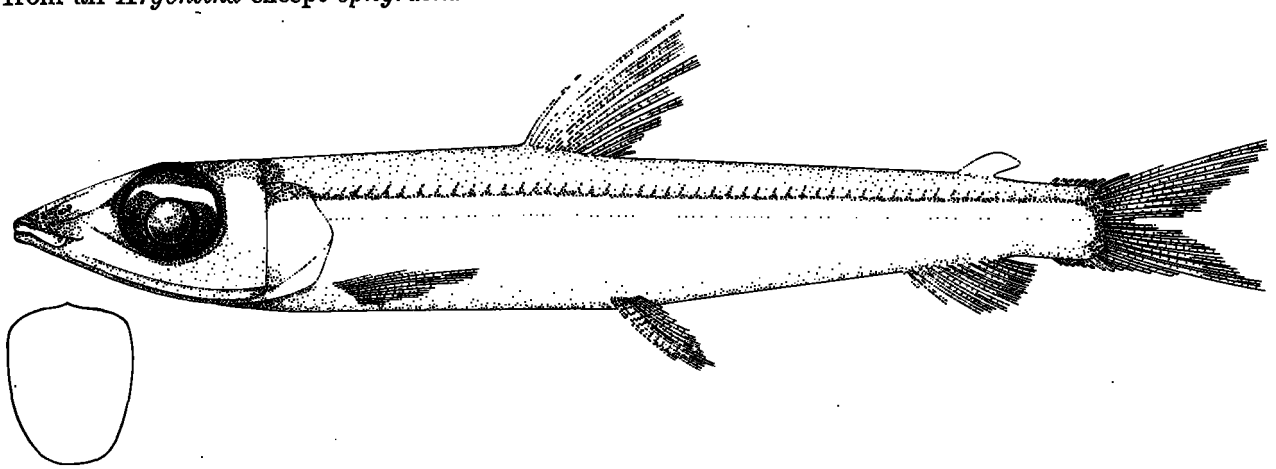

FIGURE 13.—*Argentina brucei*, USNM 159357, paratype, 128 mm. standard length. Scales not shown. Cross section from in front of dorsal fin. From Cohen, 1964, as *A. striata*.

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maxillary lies under the lachrymal. The distal end of the maxillary extends at least to the midpoint of the snout and in some specimens farther. The jaws are broadly rounded; the lower, which often has a slightly bony protuberance at the symphysis, is included. The palatine and the head of the vomer bear small, closely spaced, needlelike teeth, in a continuous band 2 to 5 teeth wide, about 55 on the head of the vomer and 70 on each palatine; no dentary teeth. The ceratobranchial of the fifth gill arch bears 8 small, conical teeth; two patches of similar teeth, 10 on the anterior patch and 14 on the posterior patch, are found at the anterior end of the fourth suprabranchial. The tongue bears eight strong, recurved teeth (description of dentition based on a single alizarin specimen). The gill rakers are medium-sized, widely spaced, and compressed at the base. The longest gill rakers are equal to one-seventh to one-eighth of the interorbital distance.

The pectoral fin originates on the dorso-lateral curve of the body close to the level of the posterior margin of the opercle. The distance between the innermost rays of the pectoral fins is generally less than the least depth of the caudal peduncle. The pectoral fin extends at least half the distance from the pectoral origin to the ventral fin origin.

The scales are deciduous and lack spines. Scale pocket counts are difficult on this soft-bodied fish; however, we estimate about 48 lateral line scales.

The peritoneum is peppered with large, dark chromatophores; however, they are not so densely distributed that they give the peritoneum a completely black appearance. The gut is immaculate. Eight to 10 pyloric caeca are present in 12 specimens; many body cavities are heavily invested with fat. The swimbladder usually begins slightly anterior to the hind curve of the stomach and terminates slightly beyond the origin of the ventral fins. Six specimens of about one hundred had silvery swimbladders; otherwise, bladders lack pigment.

Pigmentation of adult specimens preserved in formaldehyde solution is a light straw color below the lateral line, somewhat darker along the upper third of the body. The duskiness is not continuous over the dorsum. Many examples carry 8 to 12 indistinct dusky blotches on the upper part of the body. The throat, breast, and belly are unpigmented (fig. 10), although a few specimens have a light sprinkling of chromatophores at the bases of the pectoral and ventral fins. The peritoneum shows through the midventral line in some specimens.

Distribution

A. brucei has been taken on the north coasts of Hispaniola and Puerto Rico; off Jamaica, Honduras, Nicaragua, Costa Rica, and Panama; and along the north coast of South America. It has also been trawled at several localities off the mouths of the Orinoco.

Depth distribution ranges from 100 to 300 fm. (183–549 m.); however, the fish has been most often caught between 100 and 230 fm. (183–421 m.).

Habits

A. brucei has been taken only with a bottom trawl, over a mud bottom, at bottom temperatures ranging from 50° to 64° F. (10°–17.8° C.). The fish is caught more often in aggregations than singly. *A. brucei* has been taken in mixed collections with all three of the other tropical western Atlantic species, *striata*, *georgei*, and *stewarti*, though with only one at a time.

Name

Named for the well-known ichthyologist Bruce B. Collette, who helped collect many of the specimens upon which this description is based.

Study Material

All from the Atlantic. Holotype: USNM 203029, 117 mm. standard length; *Oregon* 3584, 9°13′ N., 81°30′ W., 200 fm. (366 m.), May 25, 1962. Paratypes:

Central America.—USNM 187817 (3 specimens), *Oregon* 3595, 9°02′ N., 81°26′ W., 100 fm. (183 m.). USNM 187789 (16) and TABL 100571 (6); *Oregon* 3598, 9°03′ N., 81°22′ W., 200 to 220 fm. (366–402 m.). USNM 203047 (5); *Oregon* 3597, 9°04′ N., 81°25′ W., 150 to 160 fm. (274–293 m.). USNM 187833 (7); *Oregon* 3585, 9°12′ N., 81°30′ W., 135 to 140 fm. (247–256 m.). USNM 187837 (1); *Oregon* 3584, data as for holotype. USNM 187753 (1); *Oregon* 3590, 9°18′ N., 80°22′ W., 125 fm. (229 m.). USNM 200429 (5, 1 cleared and stained); *Oregon* 5738, 9°14′ N., 79°07′ W., 120 fm. (220 m.). USNM 188016 (5); *Oregon* 3610, 12°23′ N., 82°29′ W., 200 fm. (366 m.). USNM 203031 (4); *Oregon* 3574, 12°31′ N., 82°21′ W., 200 fm. (366 m.). USNM 187793 (7); *Oregon* 3570, 14°08′ N.,

81°55′ W., 200 to 240 fm. (366–439 m.). TABL 100566 (1); *Oregon* 3615, 14°16′ N., 81°55′ W., 200 fm. (366 m.). USNM 185093 (1) and FMNH 74571 (3); *Oregon* 1868, 16°36′ N., 82°37′ W., 175 fm. (320 m.). USNM 159353 (1); *Oregon* 1871, 16°39′ N., 82°26′ W., 250 fm. (457 m.). ANSP 98604 (14); *Oregon* 3626, 16°45′ N., 81°27′ W., 150 fm. (274 m.). TABL 100562 (3); *Oregon* 3627, 16°50′ N., 81°21′ W., 200 fm. (366 m.). FMNH 66218 (2); *Oregon* 1883, 16°52′ N., 81°30′ W., 200 fm. (366 m.).

South America.—USNM 159356 (3); FMNH 66222 (2); *Oregon* 1985, 9°41′ N., 59°47′ W., 150 fm. (274 m.). USNM 159357 (9) and UF 8026 (4); *Oregon* 1989, 9°45′ N., 59°45′ W. UF 5237 (6) and FMNH 66221 (6); *Oregon* 1983, 9°43′ N., 59°53′ W., 125 fm. (229 m.). USNM 203049 (1); *Oregon* 4465, 10°45′ N., 66°37′ W., 125 fm. (229 m.). USNM 203032 (1); *Albatross* 2700, 10°59′ N., 66°00′ W., 140+ fm. (256+ m.). MCZ 45937 (6); *Oregon* 4838, 11°09.5′ N., 74°24.5′ W., 170 to 180 fm. (311–329 m.). TABL 100568 (1); *Oregon* 4858, 11°09′ N., 74°25′ W., 160 fm. (293 m.). USNM 188973 (2); *Oregon* 4860, 11°09′ N., 74°26′ W., 155 to 160 fm. (284–293 m.). USNM 203033 (1); *Oregon* 4410, 11°52′ N., 69°27′ W., 230 fm. (421 m.). USNM 203048 (2); *Oregon* 4408, 11°53′ N., 69°28′ W., 230 fm. (421 m.). USNM 203030 (2); *Oregon* 4407, 11°59′ N., 69°30′ W., 230 fm. (421 m.).

Antilles.—TABL 100570 (4); USNM 187838 (14); *Oregon* 3549, 17°50′ N., 77°52′ W., 170 fm. (311 m.). USNM 186355 (1) and FMNH 66227 (1); *Oregon* 2653, 18°18′ N., 67°18.5′ W., 300 fm. (549 m.). USNM 186354 (1); *Oregon* 2656, 18°24′ N., 67°15′ W., 100 fm. (183 m.). MCZ 40588 (4); FMNH 66228 (5); *Oregon* 2658, 18°26′ N., 67°11.5′ W., 175 fm. (320 m.). USNM 186352 (2); *Oregon* 2664, 18°31.5′ N., 66°46.5′ W., 160 fm. (293 m.). USNM 186353 (1); *Oregon* 2665, 18°31.5′ N., 66°50′ W., 180 fm. (329 m.). USNM 186357 (1) and FMNH 66229 (1); *Oregon* 2666, 18°32′ N., 66°46.5′ W., 200 fm. (366 m.). TABL 100565 (2); *Silver Bay* 5161, 19°57′ N., 71°05′ W., 190 fm. 348 m.).

ARGENTINA EUCHUS COHEN

Figure 2

A. euchus was originally described from only two specimens (Cohen, 1961). On the basis of an additional 15, we here present a new diagnosis and counts and measurements as well as a range extension.

Diagnosis

A. euchus differs from *sphyraena* and *silus* in its smooth instead of spiny scales and by its five instead of six branchiostegals. It differs from *sphyraena*, *silus*, *sialis*, *aliceae*, *elongata*, and *brucei* in having six gill rakers on the lower arm of the first arch rather than seven or more. It has 47 or 48 vertebrae, more than *aliceae* and *brucei*, which have 43 to 46; and fewer than *silus*, *elongata*, *australiae*, *kagoshimae*, and *stewarti*, which have 49 to 67. It differs from *sialis* and *australiae* in having 16 to 18 pectoral rays rather than 11 to 14. It differs from *silus*, *striata*, *georgei*, *brucei*, and *stewarti* in having 10 or 11 ventral rays rather than 12 or more.

Counts

See tables 1 to 7.

Measurements

Based on 14 specimens, 123 to 154 mm. standard length, given as percent of standard length. Preanal 82.4 (81.2–83.6); maxillary width 1.6 (1.4–1.8); depth at dorsal fin 13.5 (11.9–15.3); head depth 12.9 (11.7–13.8).

Discussion

The measurements given above were used, on the basis of the two types, to help separate *A. euchus* from *A. elongata*, *australiae*, and *kagoshimae* (Cohen, 1961). The additional material herein reported upon shows that with the exception of body depth and head depth in separating *euchus* from *australiae*, morphometric data are unsatisfactory in diagnosing *A. euchus*.

Four specimens examined lacked silvery pigment or iridescence on their swimbladders.

Distribution

A. euchus has been taken off Natal, southern Mozambique, and Kenya at depths ranging from 131 to 322 fm. (240–589 m.).

Study Material

All from the western Indian Ocean. USNM 203160 (1 specimen), *Anton Bruun* cruise 8, sta. 421 G, 02°56′ S., 40°28′ E. 240 m. USNM 203159 (11), MCZ (1), FMNH (1), and BMNH (1); *Anton Brunn* cruise 8, sta. 396 B, 25°32′ S., 33°24′ E., 450 to 455 m.

GENUS *GLOSSANODON* GUICHENOT

We have received material of *Glossanodon polli* from West Africa and five small fishes from the Arabian Sea that represent a species close to but distinct from *G. polli.*

GLOSSANODON MILDREDAE, NEW SPECIES

Figure 14

Diagnosis

G. mildredae differs from *pygmaeus* in having its vent immediately anterior to the anal fin base rather than farther forward, in having teeth on the dentary, and in having 23 rather than 12 to 14 pectoral rays. It differs from *leioglossus* and *semifasciatus* in having dentary teeth along more than half the distance from the symphysis to the angle of the gape. It differs from *lineatus* in having 5 instead of 4 branchiostegal rays, 13 instead of 15 anal rays, and 23 instead of 20 pectoral rays. It differs from *polli* in having at least 55 lateral line scales rather than 48 to 51. Also, *G. mildredae* has dusky blotches mainly above the midline of the body; in similar-sized *polli*, the ventral half of the side bears continuations of the dorsal blotches.

Counts and Measurements

See table 8.

Description

Greatest depth behind head, tapering little to caudal peduncle. The dorsal profile of the head is slightly interrupted by the dorsal rim of the orbit. The ventral profile of the head rises more abruptly from a point below the anterior margin of the eye. The interorbital space between the supraocular canals is flat.

The dorsal margin of the maxillary lies under the lachrymal and extends to the joint between the lachrymal and the jugal; its distal end is closer to the anterior margin of the orbit than to the snout. Lower jaw projecting slightly; both jaws are rounded, the lower less broadly.

TABLE 8.—*Counts and measurements in millimeters on type specimens of* Glossanodon mildredae

	Holotype USNM 203235	Paratype USNM 203234	Paratype USNM 203234	Paratype USNM 203234	Paratype USNM 203233
Measurements:					
Standard length	64.9	69.8	58.1	65.7	41.6
Preanal	54.1	----	48.6	53.6	32.2
Preventral	33.5	----	29.5	34.1	22.7
Predorsal	30.7	----	28.4	31.3	20.7
Head length	20.8	----	16.6	19.2	13.7
Snout	6.2	----	5.1	4.7	4.1
Eye	6.2	----	5.4	6.4	3.9
Maxillary length	5.3	----	4.0	4.6	3.1
Maxillary width	1.2	----	1.0	1.2	----
Body depth at dorsal	7.1	----	6.2	7.7	5.4
Body width behind head	7.0	----	5.3	6.5	4.2
Caudal peduncle depth	4.1	4.3	3.8	4.2	3.1
Counts:					
Dorsal fin rays	13	----	13	13	----
Anal fin rays	13	13	13	13	----
Pectoral fin rays	23	----	----	23	23
Ventral fin rays	13	12	12	12	13
Vertebrae	51	50	50	51	49
Gill rakers on lower arm first arch	----	23	23	----	----
Lateral line scales	55+	----	----	----	----
Branchiostegal rays	----	5	5	5	----

Each palatine bears 15 to 20 short, conical, widely spaced teeth, arranged in an irregular series. The head of the vomer has 10 to 12 similar teeth. The tongue lacks teeth. About 10 teeth are widely spaced in a single irregular row on each dentary, extending from the symphysis to the angle of the gape. The gill rakers are elongate, lathlike structures and are closely spaced on the gill arch. The longest rakers equal about one-half the interorbital distance.

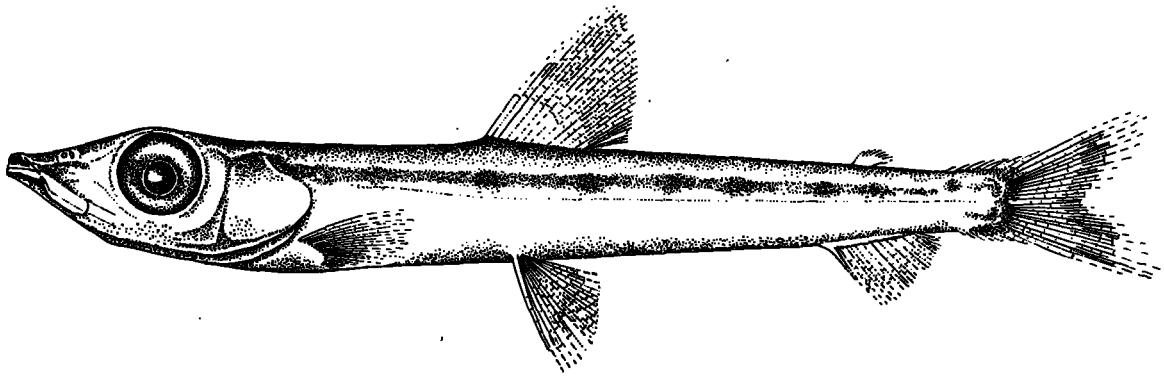

FIGURE 14.—*Glossanodon mildredae*, USNM 203235, holotype, 64.9 mm. standard length. Scales not shown. Drawn by Mildred H. Carrington.

The posterior end of the pectoral fin base forms an angle of 35 to 40 degrees with the horizontal. The tip of the pectoral fin extends at least one-third of the distance from the pectoral fin origin to the ventral fin origin. The ventral may be somewhat longer. The longest rays of the dorsal fin are longer than body depth.

Scales are lost from all four specimens; however, on the holotype we have been able to count at least 55 scale pockets along the lateral line and there are possibly 4 or 5 more.

The peritoneum is dusky. The gut is immaculate. The swimbladder lacks silvery pigment. Nine pyloric caeca are present in a single specimen.

The largest paratype (69.8 mm. standard length) has gonads containing minute, transparent eggs. We cannot say whether this fish is an immature female or a mature female with unripe gonads. If the latter, then *G. mildredae* matures at a smaller size than does *G. polli*.

The body is straw-colored, with a narrow brown band extending along the side above the midline. Spaced along the band, and broader but less well defined is a series of 8 to 10 dusky blotches, which are less distinct anteriorly. The blotches extend barely below the midline of the body. In our smallest specimen (41.6 mm. s.l.) the blotches are made of large, widely spaced chromatophores and the lateral band is very indistinct. *G. polli* of sizes comparable with our *mildredae* specimens (See fig. 8 in Cohen, 1958, taken from Poll, 1953, of a specimen 8.3 cm., probably fork length. Also USNM 203244, 61.5 mm. standard length and USNM 203243, 65.8 mm. standard length) have blotches or bands over the ventral as well as the dorsal half of the side.

Discussion

G. mildredae is closest to *G. polli*, from which it is not easily distinguished. Unfortunately, our material of *G. mildredae* is limited in quantity, size, and quality, and we have but few specimens of *G. polli* of comparable size. We doubt that one and the same species of *Glossanodon* lives in the tropical western Indian Ocean and off tropical West Africa, and we believe that at least the characters in our diagnosis serve to indicate the existence of two distinct populations.

Distribution

Known only from two localities in the tropical western Indian Ocean.

Name

Named for Mildred H. Carrington, whose tasteful and accurate drawings have contributed greatly to the progress of ichthyology.

Study Material

Holotype: USNM 203235, 64.9 mm. standard length, *Anton Bruun* cruise 9, sta. 422, 6°51′ S., 39°54′ E., 54 fm. (99 m.); 19 Nov. 1964; bottom trawl. Paratypes: USNM 203234 (3 specimens); data as for holotype. USNM 203233 (1); *Anton Bruun* cruise 9, sta. 463, 11°24′ N., 51°35′ E., 41 to 95 fm. (75–174 m.), 17 Dec. 1964, bottom trawl.

GLOSSANODON POLLI COHEN

G. polli has not been recorded since its original description (Cohen, 1958). We have examined the 18 recently collected specimens listed below and find that they agree well with the description. The two *Geronimo* specimens listed below are juveniles of 61.5 and 65.8 mm. standard lengths and show the barred pattern illustrated in the original description.

Study Material

USNM 203236 (12 specimens), MNHN (2), MCZ (1), and FMNH (1); Guinean Trawling Survey, *La Rafale*, transect 8, sta. 6, 8°28′ N., 14°21′ W., 55 fm. (100 m.). USNM 203244 (1), *Geronimo* cruise 2, sta. 213, 2°31′ S., 8°51′ E., 110 fm. (201 m.). USNM 203243 (1), *Geronimo* cruise 2, sta. 214, 2°01′ S., 8°50.5′ E., 110 fm. (201 m.)

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BATHYMETRIC MAPS AND GEOMORPHOLOGY OF THE MIDDLE ATLANTIC CONTINENTAL SHELF

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ABSTRACT

Large-scale bathymetric maps covering the northern two-thirds of the Middle Atlantic Continental Shelf have recently been published. They were compiled at a scale of 1:125,000 from 39 smooth sheets and are contoured in 1-fm. (1.8 m.) intervals on the shelf and in 10-fm. (18.3 m.) intervals on the upper slope.

Part 1 of this report discusses the construction and reliability of these maps. In addition, a short review of surveys made in the mapped area is given, a few uses for the maps are suggested, and the reliability diagrams (which appear on each map) are explained.

Part 2 discusses the past geologic history, the general distribution of sediments, and the major geomorphic processes at work in the area. In addition, the several physiographic regions and features on the Middle Atlantic Shelf are described in terms of their topography and sediments.

The Middle Atlantic Continental Shelf is one of the world's most studied shelf areas. The 60,000 square nautical miles[1] of drowned coastal lowland making up its surface have long been of interest to mariners, commercial fishermen, and scientists. Numerous nautical chart surveys, oceanographic studies, and geophysical, geological, and biological investigations have been made in the area (Geyer, 1948; Drake, Ewing, and Sutton, 1959; Heezen, Tharp, and Ewing, 1959; Murray, 1961; Drake, Heirtzler, and Hirshman, 1963; Stearns, 1963; Uchupi, 1963; Livingstone, 1965; and Emery, 1966b).

The Middle Atlantic Continental Shelf borders one of the world's largest concentrations of human activity. Called Megalopolis by Gottmann (1961), this region contains almost one-fifth of the population of the United States and is a vast market for marine resources of all kinds. The shelf supplies Megalopolis with commercial and sport fisheries, recreation on the seashores, mineral resources, and space for waste disposal. The need for detailed bathymetric maps in the study of Continental Shelf geology, geomorphology, and mineral resources is well known (Veatch and Smith, 1939; Emery and Schlee, 1963; Emery, 1966b). Less widely appreciated, but equally important, are the uses of such maps in the synthesis and study of physical and biological data.

The shape of the sea floor can influence the movement of water masses on the shelf, and this movement can affect the distribution of such oceanographic properties as temperature, salinity, and nutrient elements (Bigelow, 1931; Hachey, Lauzier, and Bailey, 1956; Trites, 1956). Although only a few benthonic animals are known to respond directly to the shape of the bottom (e.g., see Yonge, 1962), all marine animals respond to the distribution of water-mass properties, which are affected by the bottom. Hence, definite correlations exist between the shape of the bottom and the locations of marine animals (see Parker and Curray, 1956), and detailed studies of environmental relations on the shelf require a detailed knowledge of bathymetry.

[1] I use English fathoms and nautical miles throughout the paper because all the data were collected in English rather than metric units. For conversion, 1 fm. equals 1.83 m., and 1 nautical mile equals 1.85 km.

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Large-scale bathymetric maps covering the northern two-thirds of the Middle Atlantic Continental Shelf (fig. 1) have recently been published by Stearns and Garrison (1967). These maps are contoured in 1-fm. intervals from the shore to 100 fm. and in 10-fm. intervals from 100 to 500 fm. and are drawn on a Mercator projection at a nominal scale of 1 : 125,000.

The present maps can be used in a variety of ways, such as (1) interpolation aids when mapping physical data, (2) foundations for the analysis of relations between physical features and biological distributions, and (3) sources of information for the efficient planning of stratified sampling programs and surveys.

The purpose of this paper is to describe these maps, their construction and reliability, and to discuss the geomorphology of the mapped region.

PART 1. BATHYMETRIC MAPS

The proper use of bathymetric maps requires some knowledge of how they were made, as well as an estimate of their reliability. These topics are discussed in this part of the report.

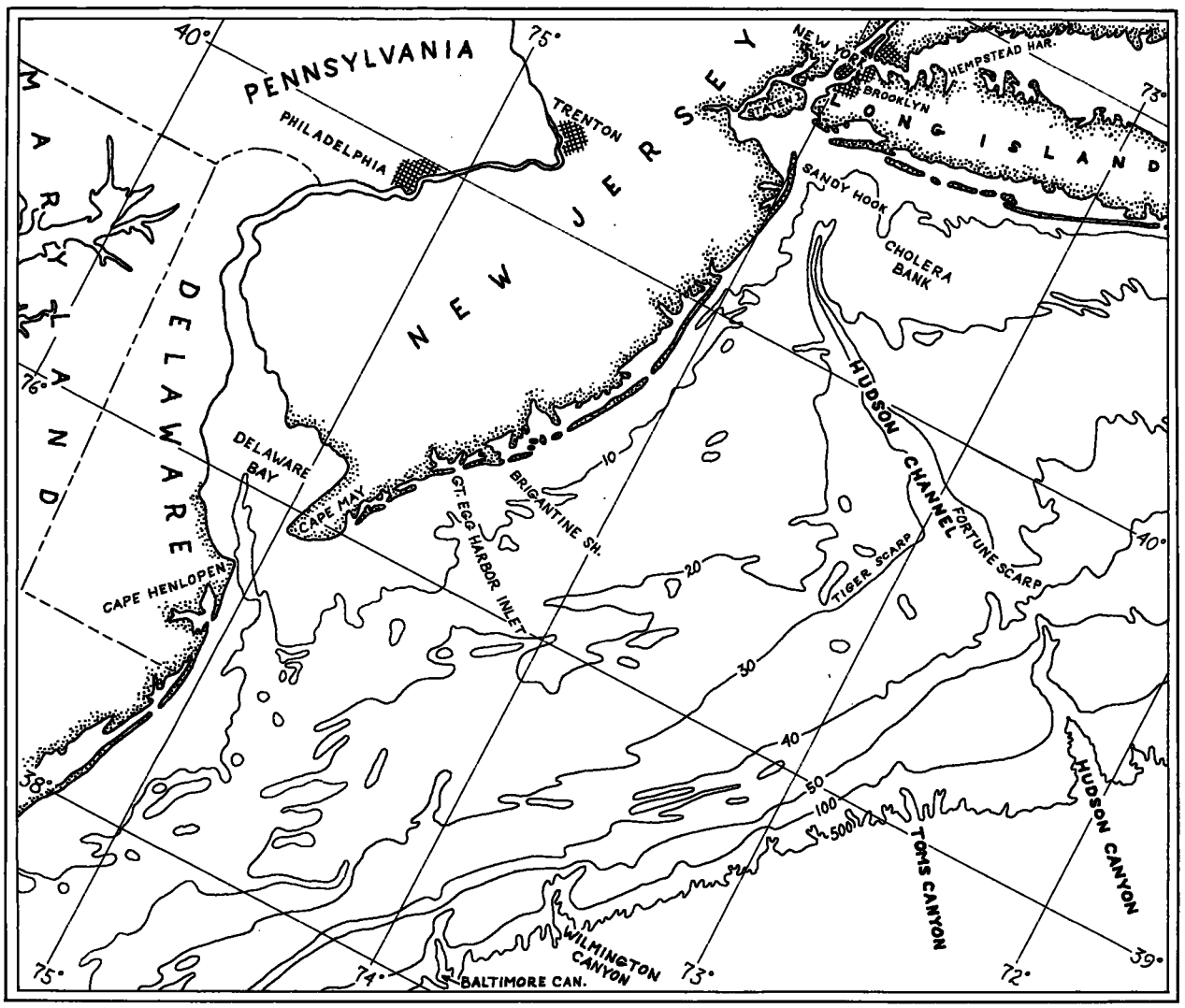


FIGURE 1.—Generalized bathymetry of the Middle Atlantic Continental Shelf and locations of major features discussed in the text. Depth contours in fathoms. Sources: USCGS Chart 1000 (13th ed., 1949) and Stearns and Garrison (1967).

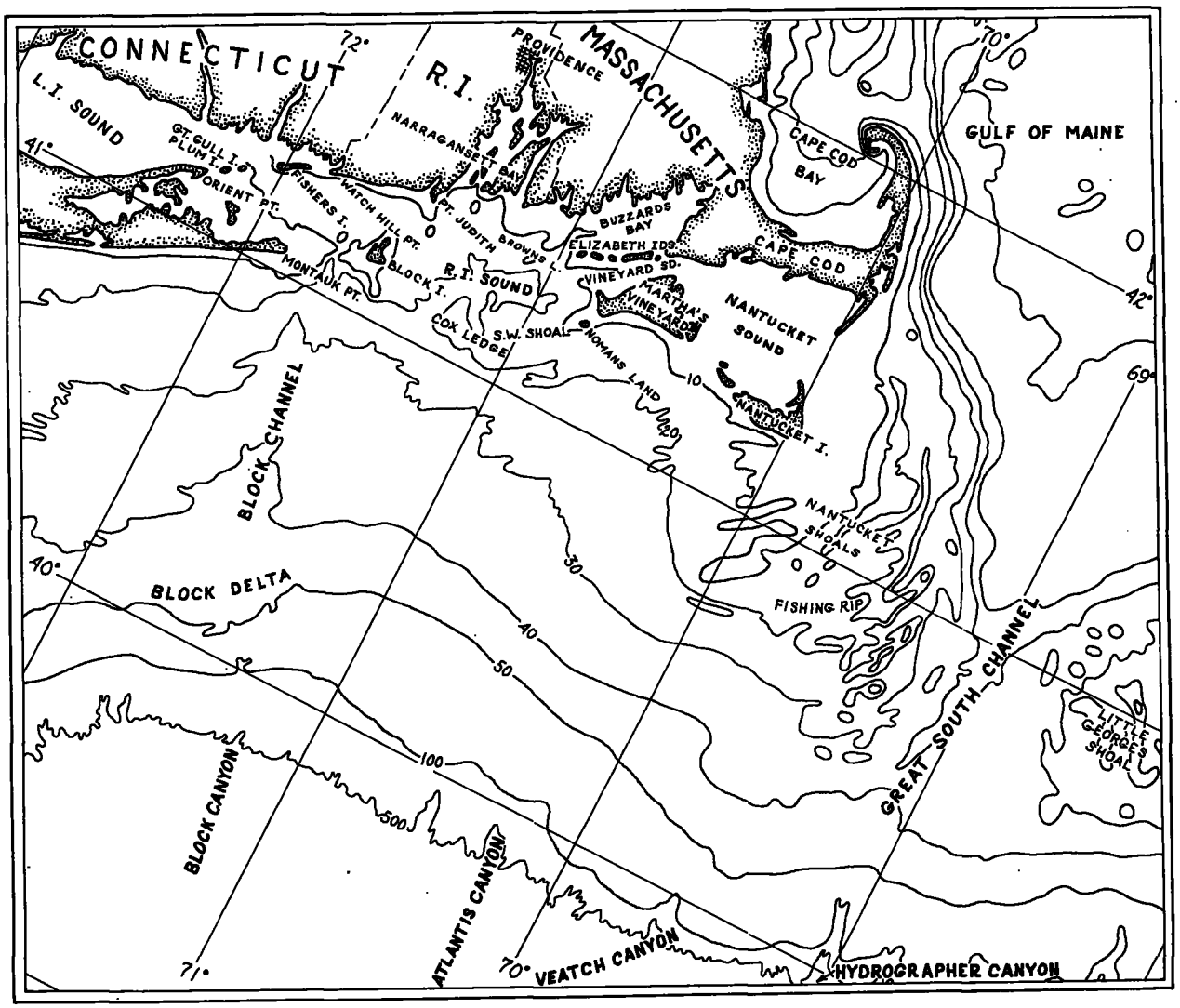
CONSTRUCTION OF THE MAPS

Construction of the maps is discussed from three aspects: (1) history of past surveys, (2) study of present surveys, and (3) methods of construction.

Past Bathymetric Surveys

The first systematic bathymetric survey of the entire width of the Middle Atlantic Continental Shelf was made by the U.S. Coast Survey in 1842 (USCGS Hydrographic Survey no. 100, scale 1:400,000). Previously, only some inshore areas had been systematically surveyed, and charts of the offshore regions were based on a few isolated soundings. The 1842 survey covered the area between Rhode Island Sound and Cape May and from near shore to a little over 100 fm. It was supplemented in 1844 by a survey covering much the same area (no. 101, scale 1:400,000) and again in 1859 by a survey extending from Martha's Vineyard to slightly south of Cape Henlopen, Del. (no. 670, scale 1:400,000).

No surveys were made during the Civil War, but in the 1870's and 1880's much sounding was



done on the Continental Slope and in the adjacent ocean basins, largely as a result of (1) an increased interest in the life of abyssal regions, (2) increasing activity in the laying of submarine telegraph cables, and (3) the development of deep sea wire-sounding machines (Agassiz, 1888; Tanner, 1897). From 1877 to 1880 Alexander Agassiz (1888) directed surveys aboard the Coast Survey ship *Blake* along the Atlantic Continental Slope, but it was not until 1882 that the shelf itself was again surveyed, this time from Montauk Point, Long Island, to Cape Henlopen, Del. (no. 1558, scale 1:300,000). This survey was extended south to Cape Charles in 1886 (no. 1720, scale 1:200,000) and to the east as far as Georges Bank during 1887–1889 (nos. 1782, scale 1:300,000; and 1837, scale 1:400,000). In all of these early surveys, the soundings were by lead line and the navigation was by shore sightings, astronomical fixes, and dead reckoning.

Except for a few isolated investigations of shoal areas, the Middle Atlantic Shelf was not again systematically surveyed until the 1930's, when new sounding and navigational methods had been developed. These surveys, from Georges Bank to Cape Henry and from the shore to the Continental Slope and Rise, are the principal sources used for constructing the maps discussed in this paper.

Several earlier bathymetric maps were based on the surveys of the 1930's. The first and most famous are the maps of Veatch and Smith (1939)—see also Smith (1939). These authors compiled a series of charts of the Continental Slope from Georges Bank to Chesapeake Bay and of the Hudson Channel region of the shelf (scale 1:120,000). Uchupi (1965), in cooperative work by the Woods Hole Oceanographic Institution and the U.S. Geological Survey, used the surveys to compile a 1:1,000,000 scale map of the shelf, slope, and rise from southern Canada to the Straits of Florida. In addition, the USCGS has used the surveys to construct nautical charts of the region at scales of 1:80,000 and 1:400,000 (see the 1100 and 1200 series of nautical charts). The surveys have also been used for small maps, published as text illustrations (e.g., Elliott, Myers, and Tressler, 1955; Garrison and McMaster, 1966).

Present Data Sources

The data from 39 USCGS hydrographic surveys, made between 1932 and 1961, were used for making the present maps. (The smooth sheets of these surveys vary in scale from 1:20,000 to 1:120,000.) In addition, 25 published USCGS nautical charts (scales 1:10,000 to 1:80,000) were used for some nearshore areas, bays, sounds, and harbors. The land contours which appear on some sheets were compiled from U.S. Geological Survey and Army Map Service topographic quadrangle maps (scales 1:24,000 and 1:62,500). The Long Island contours are from a topographic map of the Island, scale 1:125,000, appearing in Fuller (1914).

More bathymetric information exists than was used in the present compilation. Many miles of sounding lines have been run on the Middle Atlantic Continental Shelf by the research ships of various government agencies, private research institutions, and universities. Many of these data are equal in quality to those used, but most have not been reduced and plotted in a form that can be readily contoured.

The new developments in the surveys of the 1930's were echosounding and radio-acoustic ranging. Echosounding was developed in both the United States and Europe during the first part of this century, and by 1923 the USCGS had installed their first echosounder. This method of measuring depths was rapidly improved and soon replaced the older lead line and wire-sounding machine. Before the 1930's, positions were determined in much the same manner as they were in 1842 and before. During the early 1920's, offshore positioning had developed into an elaborate system of precise dead reckoning, but it was not until the USCGS introduced radio-acoustic ranging in 1924 that methods of navigation were changed fundamentally (Adams, 1942). This new method was continually improved throughout the surveys of the 1930's and was replaced by wholly electronic systems during the 1940's.

Methods of Construction

Bathymetric contour lines were drawn directly on either (1) full-scale, corrected copies of the original surveys (smooth sheets), or (2) on nautical charts of nearshore areas. Louis E. Garrison contoured the area between about long. 69°25′ and 72°00′ W. and shallower than about 100 fm. (USCGS Hydrographic Surveys 6331, 6347, 6440, 6441, and 6447). I contoured the rest of the area.

This contoured source material was transferred

by pantograph to dimensionally stable plastic compilation sheets at a uniform scale of 1:125,000 (Mercator projection, scale of 1:125,000 at lat. 40° N.); each sheet covered 1° of latitude and longitude. Transfer was done in stages for each piece of source material; small quadrangles were transferred independently to minimize distortion of scale and paper. Adjustment and matching between surveys, corrections, and final smoothing of the isobaths were done on the compilation sheets. The USCGS made the final map layout and design.

RELIABILITY OF THE MAPS

Present technology makes it impractical to observe large areas of the sea floor directly; thus, bathymetric maps are necessarily interpretive drawings of an invisible surface (for discussions of this subjective element in bathymetric mapping see Veatch and Smith, 1939; Jones, 1941; and Shepard, 1943). Such maps are usually made from discrete soundings, between which assumed depths must be interpolated before contour lines of constant depth (isobaths) can be drawn. The uncertainty of these assumed depths, plus observational and positional errors in the original soundings, makes exact correspondence between a bathymetric map and the real sea floor an impossibility. The user of a map, however, should know what accuracy to expect.

The following paragraphs of this section discuss the evaluation of the reliability of the maps, the reliability diagrams which appear on each map, and the spatial distribution of the map errors.

A general method for quantitative estimate of the reliability of isoline maps has been presented by Stearns (1968). In this general method the reliability of isolines (expressed as a variance) is related to (1) observational errors, (2) positional errors, (3) interpolation errors, (4) errors in the time of an observation, (5) synopticity errors (errors due to lack of simultaneity in the observations), and (6) the space-time rates-of-change and the directions of the gradients of the mapped variable.

In applying the method to the present bathymetric maps, I considered all the above factors, with the exception of time and synopticity errors. I omitted the time-dependent errors, first, because little exact information is available on the rates-of-change of bottom topography, and, second, because such changes, except in limited areas, are likely to be very small during the period of useful life of the maps.

The reliability equations (Stearns, 1968), with the time-dependent terms omitted, are as follows:

$$\bar{\epsilon}_3=\bar{e}_0+\bar{e}_p\bar{g}_p\,\overline{\mathrm{Cos}}\,\gamma_p+\bar{e}_l\bar{g}_l\,\overline{\mathrm{Cos}}\,\gamma_l+\bar{e}_l'\bar{g}_l'\,\overline{\mathrm{Cos}}\,\gamma_l' \tag{1}$$

which expresses the expected bias of the values of the isobaths at any point on the map or within any subarea of the map, and

$$\begin{aligned}V_{\epsilon_3}=&V_{\epsilon_0}+V_{\epsilon_p}(V_{g_p}+\bar{g}_p^2)\,(V_{\mathrm{Cos}\,\gamma_p}+\overline{\mathrm{Cos}^2}\,\gamma_p)\\&+\bar{e}_p^2(V_{g_p}[V_{\mathrm{Cos}\,\gamma_p}+\overline{\mathrm{Cos}^2}\,\gamma_p]+\bar{g}_p^2V_{\mathrm{Cos}\,\gamma_p})\\&+V_{\epsilon_l}(V_{g_l}+\bar{g}_l^2)\,(V_{\mathrm{Cos}\,\gamma_l}+\overline{\mathrm{Cos}^2}\,\gamma_l)\\&+\bar{e}_l^2(V_{g_l}[V_{\mathrm{Cos}\,\gamma_l}+\overline{\mathrm{Cos}^2}\,\gamma_l]+\bar{g}_l^2V_{\mathrm{Cos}\,\gamma_l})\\&+V_{\epsilon_l'}(V_{g_l'}+\bar{g}_l'^2)(V_{\mathrm{Cos}\,\gamma_l'}+\overline{\mathrm{Cos}^2}\,\gamma_l')\\&+\bar{e}_l'^2(V_{g_l'}[V_{\mathrm{Cos}\,\gamma_l'}+\overline{\mathrm{Cos}^2}\,\gamma_l']+\bar{g}_l'^2V_{\mathrm{Cos}\,\gamma_l'})\end{aligned} \tag{2}$$

which expresses the variance of the values of the isobaths at any point, or within any subarea, on the map.

These equations may be evaluated for a map as a whole (in which case a single average reliability value would be obtained), or for any arbitrarily selected small portion of a map. For the present maps, the equations were evaluated for each adjacent unit area of 5 geographical minutes to a side. This unit area was selected as a compromise between the geographic diversity of the map's reliability and the time available for manual computation. Over 1,600 unit areas were involved in the evaluation.

Evaluation of the Reliability

The evaluation of the terms in equations 1 and 2 are discussed in this section.

Observational errors (e_o).—The echosoundings made during the surveys of the 1930's and used as the basis for constructing most areas of the present maps were evaluated by Veatch and Smith (1939)—see also Adams (1942). They concluded (p. 60) that the accuracy of these soundings was within 1 part in 100 for areas deeper than 100 fm. and within 1 part in 200 for areas shallower than 100 fm. To approximate maximum errors on the shelf proper, I used their larger estimate, 1

part in 100, for all depths (0 to 500 fm.) and for all surveys and nautical charts used in the compilation.

Because of lack of data on bias in the soundings, I assumed unbiased work; hence, $\bar{e}_o$ was taken to be zero. The variance of the observational errors was estimated by assuming that the errors are normally distributed and that the value, 1 part in 100, represents 99 percent of the total distribution (this assumption implies that systematic and personal errors have been removed from the data and that any reduction errors have a random distribution). Therefore,

$$\pm d/100 = \pm 2.576\sqrt{V_{e_o}};\ \text{hence}\ V_{e_o} = 0.000015d^2$$

where the variable d equals the maximum depth, in fathoms, within each 5-minute unit area.

To account for round-off errors, I added a constant factor to each variance value. This factor was 0.083 fm. when the soundings were recorded to the nearest fathom and 0.0023 fm. when recorded to the nearest foot. I assumed a rectangular, or uniform, distribution of these errors; hence, the variance equals $E^2/3$ (see Weatherburn, 1961, p. 14), where E equals one half of the round-off interval.

Positional errors (e_p).—Veatch and Smith (1939) discussed the accuracy of positioning for the radio-acoustic ranging methods used in the surveys of the 1930's (see also Adams, 1942). They concluded (p. 65) that the accuracy was 1 part in 200 for distances less than 100 nautical miles from the control (reference) points used in a survey. To approximate a maximum estimate of positional errors, I used 1 part in 100 for all of the surveys (except for a few recent ones which cover a large part of Nantucket Shoals) and all the nautical charts.

Again, because of lack of data, I assumed unbiased work; hence $\bar{e}_p$ was taken to be zero. The variance of the positional errors was determined in the same way as described above for observational errors; hence $Ve_p = 0.000015D^2$, where the variable D equals the maximum distance in nautical miles between each 5-minute unit area and the nearest control point (sonobuoy or station vessel) used in a survey. For nearshore nautical charts the distance D was measured to the nearest prominent shore feature.

To each variance value I added a constant factor—0.0045 nautical mile, to account for such cartographic errors as paper distortion and misalignments in tracing and printing. This factor was calculated by assuming a normal distribution of cartographic errors with a 99 percent limit of ±0.1 inch or ±0.17 nautical mile at a scale of 1 : 125,000.

For the recent surveys on Nantucket Shoals (1959–61), during which electronic positioning systems were used, I assumed a 99 percent error of ±0.066 nautical mile (±400 feet) and a normal error distribution; hence $Ve_p = 0.0007$ nautical mile. To this was added the cartographic error variance of 0.0045 nautical mile giving a constant total error variance of 0.0052 nautical mile for these surveys.

Interpolation errors (e_l *and* $e_{l'}$).—If we were concerned with maps showing only the depths of soundings, the total error would be a simple combination of the positional and observational errors discussed above. Because, however, we are dealing with isobath maps, interpolation errors must also be considered. These errors are of two kinds: (1) those associated with depths interpolated along axes between actual soundings (primary interpolation error, e_l) and (2) those associated with depths interpolated between the primary interpolation axes (secondary interpolation error, $e_{l'}$).

The equations for computing these interpolation errors are (Stearns, 1968):

$$\bar{e}_l = \bar{e}_{l'} = 0 \tag{3}$$

$$V_{e_l} = \tfrac{1}{6}(V_l + \bar{l}^2) \tag{4}$$

$$V_{e_{l'}} = \tfrac{1}{6}(V_{l'} + \bar{l}'^2) \tag{5}$$

These are based on a simple two-point linear interpolation scheme.

The evaluation of V_{e_l} and $V_{e_{l'}}$ depends on the particular survey pattern used. The quantity $(V_l + \bar{l}^2)$ in equation 4 is the mean sum of the squares of the distances between the soundings. For a rectangular array of discrete soundings along more or less parallel track lines, as is the situation for most of the hydrographic surveys of the Middle Atlantic Continental Shelf, this quantity equals $\frac{1}{2}(a^2+b^2)$, where a is the distance between track lines and b is the distance between soundings on each line. By taking the mean of five systematic samples of the two distances, I estimated the quantities a and b for each 5-minute unit area.

The quantity $(V_{l'}+\bar{l}'^2)$ in equation 5 is the mean sum of the squares of the distances between the primary interpolation axes. Several choices are possible for secondary interpolation axes (Stearns, 1968). The correct choices are those axes actually used by the cartographer in drawing the map. A human being, however, in his subjective approach to contouring, is seldom fully aware of just what axes he has used. Therefore, in computing the reliability of the present maps, I assumed that the shortest axes were used, which, in the rectangular trackline surveys of the Middle Atlantic Continental Shelf, equaled the distance between soundings. These distances are usually equal within any unit area, so the quantity $(V_{l'}+\bar{l}'^2)$ equals b^2.

The topographic slopes.—Positional and interpolation errors (which are expressed in distance units) are converted into depth errors, by multiplying them by g Cos γ, where g is the positive topographic slope in the vicinity of the soundings (or the interpolated point) and γ is the angle between the errors and the local slope.

The slopes g_p, g_l, and $g_{l'}$ were assumed to be equal and were estimated from five systematic samples taken in each 5-minute unit area. Each sample consisted of the maximum slope measured in a circle 1 nautical mile in diameter. The mean slope, $\bar{g}$, was taken as the mean of the five samples, and the variance of the slopes, V_g, was approximated by $(0.43\ \omega)^2$, where ω was the range of the five samples. This estimate of the variance assumed that the slopes have a normal distribution within each 5-minute unit area and was used as a computational expedient (see Dixon and Massey, 1957, pp. 273, 404).

The cosines.—In estimating the cosines in equations 1 and 2, I assumed that all angles had an equal probability of occurrence; thus γ_p, γ_l, and $\gamma_{l'}$ range from zero to π radians (from 0° to 180°), and the probability functions of the angles equal $1/\pi$. Hence,

$$\overline{\text{Cos}}\,\gamma=\frac{1}{\pi}\int_0^{\pi}\text{Cos}\,\gamma d\gamma=0$$

and

$$V_{\text{Cos}\,\gamma}=\frac{1}{\pi}\int_0^{\pi}\text{Cos}^2\gamma d\gamma=\tfrac{1}{2}$$

This assumption may be true for positional errors, because I assumed that these errors are unbiased. It is not strictly true, however, for interpolation errors, and a more accurate, although more time-consuming method could have been used; i.e., the final map could have been matched with the interpolation networks actually used and the angles measured.

The Source Diagram

The source diagram on each map shows the number, scale, and date of the USCGS hydrographic surveys and nautical charts used in the construction of the maps.

The maps depict the sea floor at the dates of the various surveys, and the user must draw his own conclusions as to changes that may have taken place since then. Significant changes are likely only along some portions of the coast above about 10 fm., in offshore shoal areas, and along the upper Continental Slope where slumping may have occurred (see Lucke, 1934a, 1934b; Howard, 1939; Heezen, 1963; Miller and Zeigler, 1964; Stewart and Jordan, 1964; Uchupi, 1967). In such areas the maps and their reliability diagrams should be used with caution.

Those who wish to study the actual soundings may examine or purchase copies of the original hydrographic survey sheets from the USCGS, Washington, D.C.

Diagram of the Mean Distance Between Track Lines

The mean distance between track lines is a common device for indicating the reliability of bathymetric maps. Reliability is usually assumed to be better where the lines are closely spaced. Trackline spacing also indicates the resolution of a survey; i.e., the minimum size of features consistently discoverable from the survey. Surveys with many different trackline spacings were used in drawing the maps. Consequently, the isobaths are more detailed in some areas than in others.

Diagram of the Standard Deviation of the Isobath Depth Error

The standard deviations in the isobath depth error diagram are estimates of how much and how frequently the depths indicated on the maps may depart from the true depths. The diagram is based on the square root of the variance given by equation 2 and shows the average standard deviation in unit areas of 5 geographical minutes to a side. It applies to depths as indicated on the maps, not to the original soundings. A more detailed diagram of the entire mapped area is reproduced in figure 2.

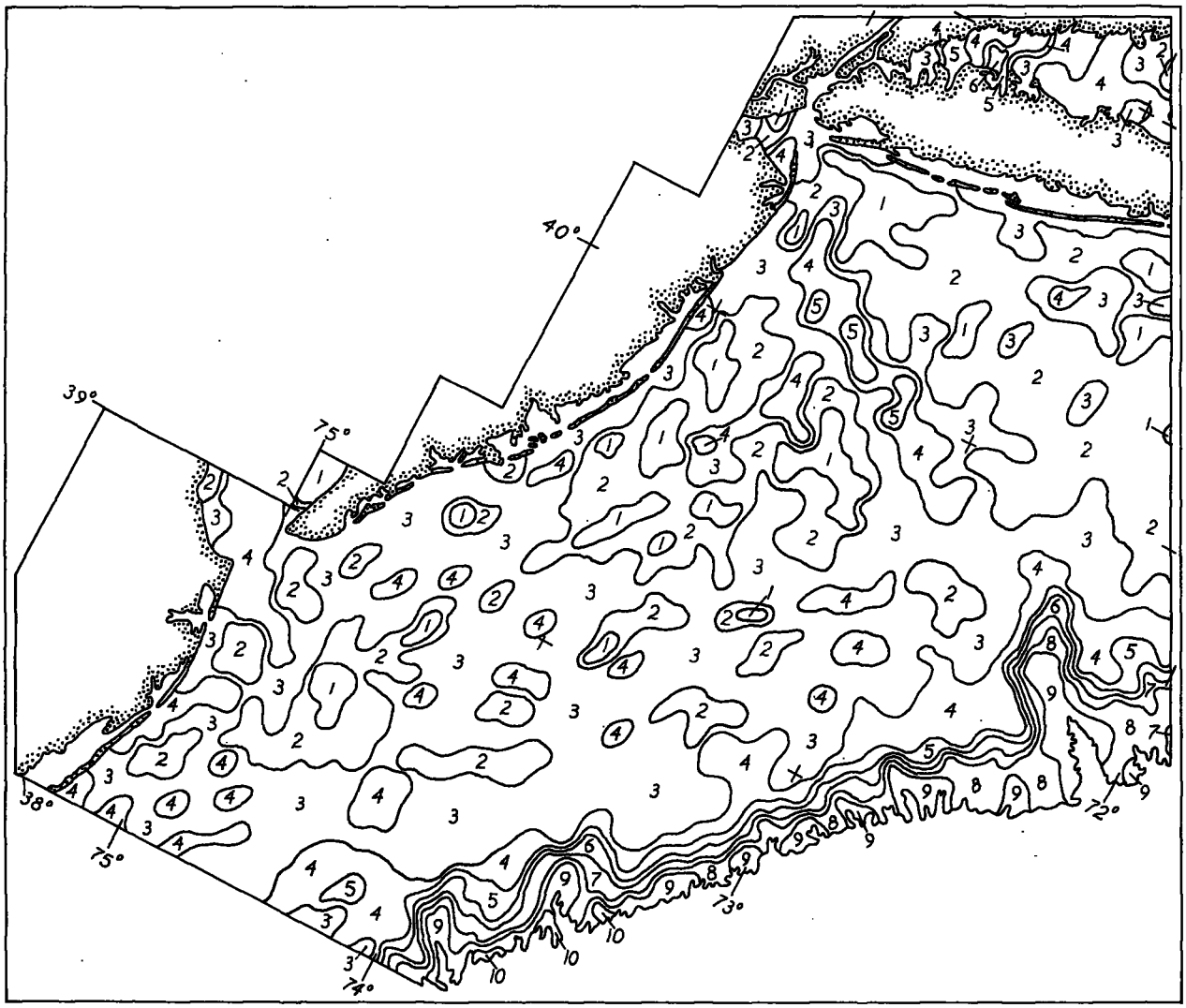
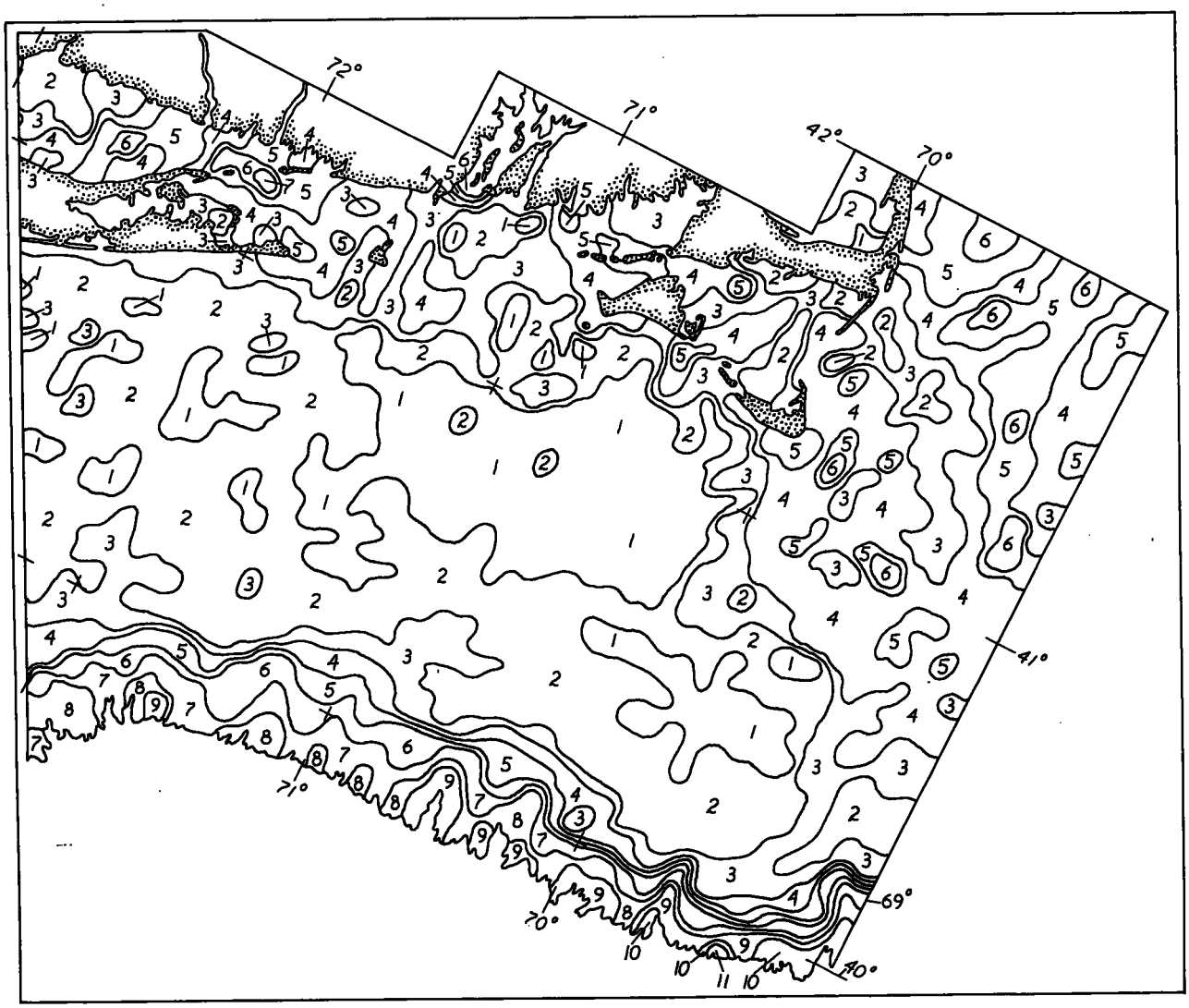


FIGURE 2.—Standard deviation of the isobath depth error. (1) Less than 0.25 fm. (2) 0.25–0.49 fm. (3) 0.50–0.99 fm. (4) 1.00–1.99 fm. (5) 2.00–3.99 fm. (6) 4.00–7.99 fm. (7) 8.00–15.99 fm. (8) 16.00–31.99 fm. (9) 32.00–63.99 fm. (10) 64.00–127.99 fm. (11) 128.00 fm. and more.

The figures in the diagram may be used to estimate the expected correspondence between the mapped depths and the true depths. This expected correspondence is expressed as a probability that the true depth falls between certain limits. For example, if we assume a normal distribution of depth errors in an area where the standard deviation of the depth error is 1 fm., then the probability is 99 percent that the indicated depth is correct to within ±2.6 fm., 90 percent that the depth is correct to within ±1.6 fm., or 50 percent that the depth is correct to within ±0.7 fm. The depth of any isobath as shown on the maps should be thought of as representing a probable range of depths rather than as a single exact depth.

The above limits were computed by the formula $r=Z_i\sigma$, where r is the expected range of depths, σ is the standard deviation taken from the depth error diagram (fig. 2), and Z_i is a number that depends upon the probability i and upon the kind of error distribution (see Dixon and Massey, 1957, or other statistics textbooks).

The above formula gives the expected range due only to errors in the map. To find the expected range when the maps are being used aboard a ship to search for a given bathymetric feature, the



standard deviation would have to include the ship's errors; i.e., $\sigma=\sqrt{\sigma_m^2+\sigma_s^2}$, where σ_m is the map standard deviation taken from the depth error diagram, and σ_s is the ship standard deviation. The ship standard deviation may be estimated as the square root of the first three terms on the right-hand side of equation 2.

Diagram of the Standard Deviation of the Isobath Position Error

The standard deviations in the isobath position error diagram are estimates of how much and how frequently the positions of the depths as indicated on the maps may depart from the true positions. This diagram is also based on the square root of equation 2; it shows the average standard deviation in 5-minute unit areas and applies only to indicated depths—not to the original soundings. The values in the diagram were computed by dividing the standard deviations of the isobath depth error (fig. 2) by $\sqrt{V_g+\overline{g}^2}$, where $\overline{g}$ is the mean topographic slope of the sea floor in a given 5-minute unit area, and V_g is the variance of the topographic slope within the same 5-minute unit area. A more detailed diagram of the entire mapped area is reproduced in figure 3.

The figures in this diagram may be used to esti-

mate the expected correspondence between the mapped positions of the depths and their true positions. This expected correspondence is expressed as a probability that the true position falls between certain limits. For example, if we assume a normal distribution of position errors in an area where the standard deviation of the position error is 0.2 nautical mile then the probability is 99 percent that a given depth will be found within ±0.5 nautical mile of its indicated position (i.e., will be found within a circle 1.0 nautical mile in diameter centered on the given depth), 90 percent that it will be found within ±0.3 nautical mile of its indicated position, or 50 percent that it will be found within ±0.1 nautical mile of its indicated position. The position of any isobath as shown on the maps should be thought of as the center of a probable range of positions rather than as a single exact position.

The above limits were computed by the same formula as was the probable range of depths, except that here r is the expected range of positions, and σ is the standard deviation taken from the position error diagram (fig. 3).

This computation also applies only to map errors. To find the expected range when the

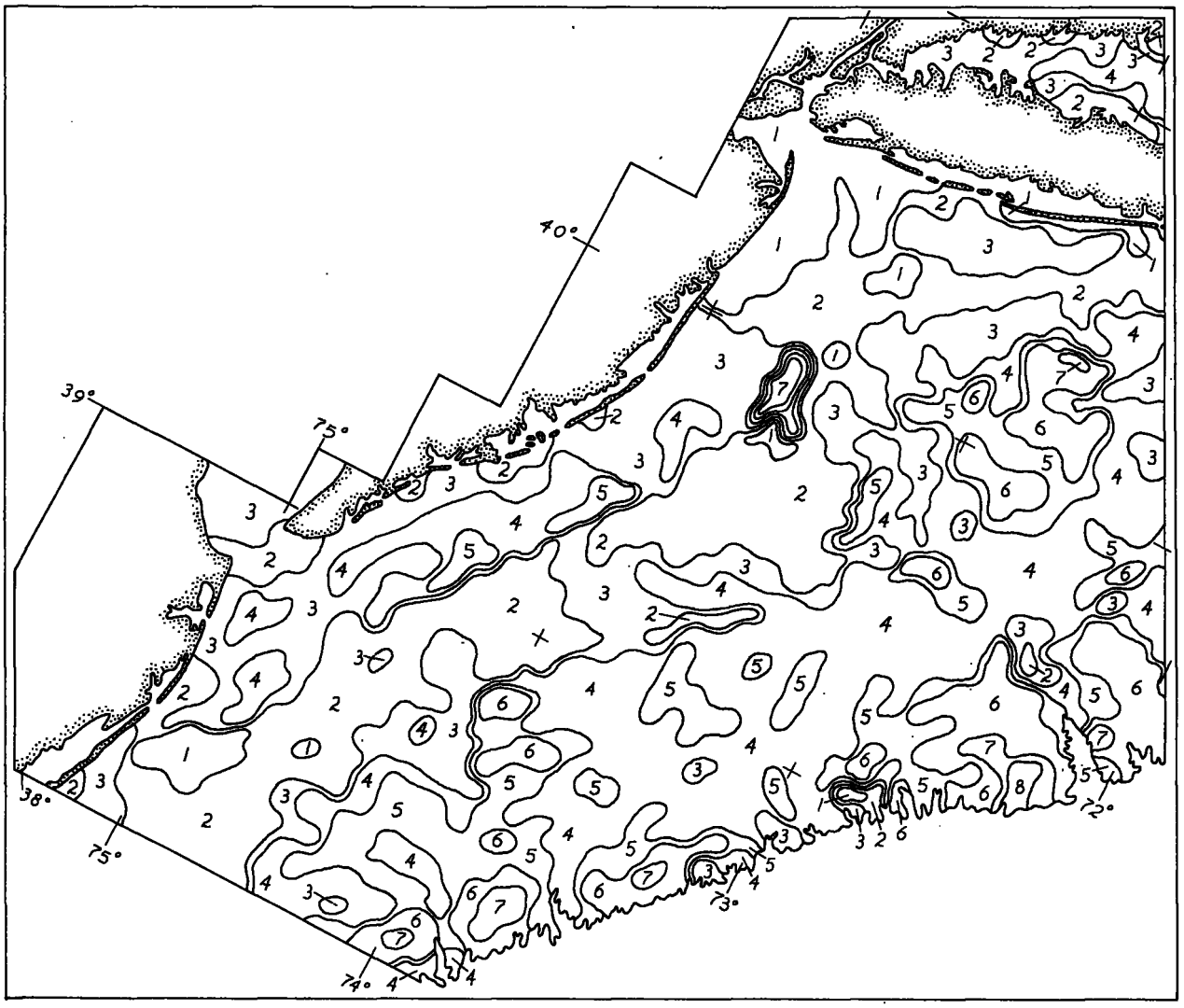


FIGURE 3.—Standard deviation of the isobath position error. (1) 0.05–0.09 nautical mile. (2) 0.10–0.14 nautical mile. (3) 0.15–0.19 nautical mile. (4) 0.20–0.24 nautical mile. (5) 0.25–0.29 nautical mile. (6) 0.30–0.39 nautical mile. (7) 0.40–0.49 nautical mile. (8) 0.50–0.59 nautical mile. (9) 0.60–0.69 nautical mile. (10) 0.70–0.79 nautical mile. (11) 0.80–0.89 nautical mile.

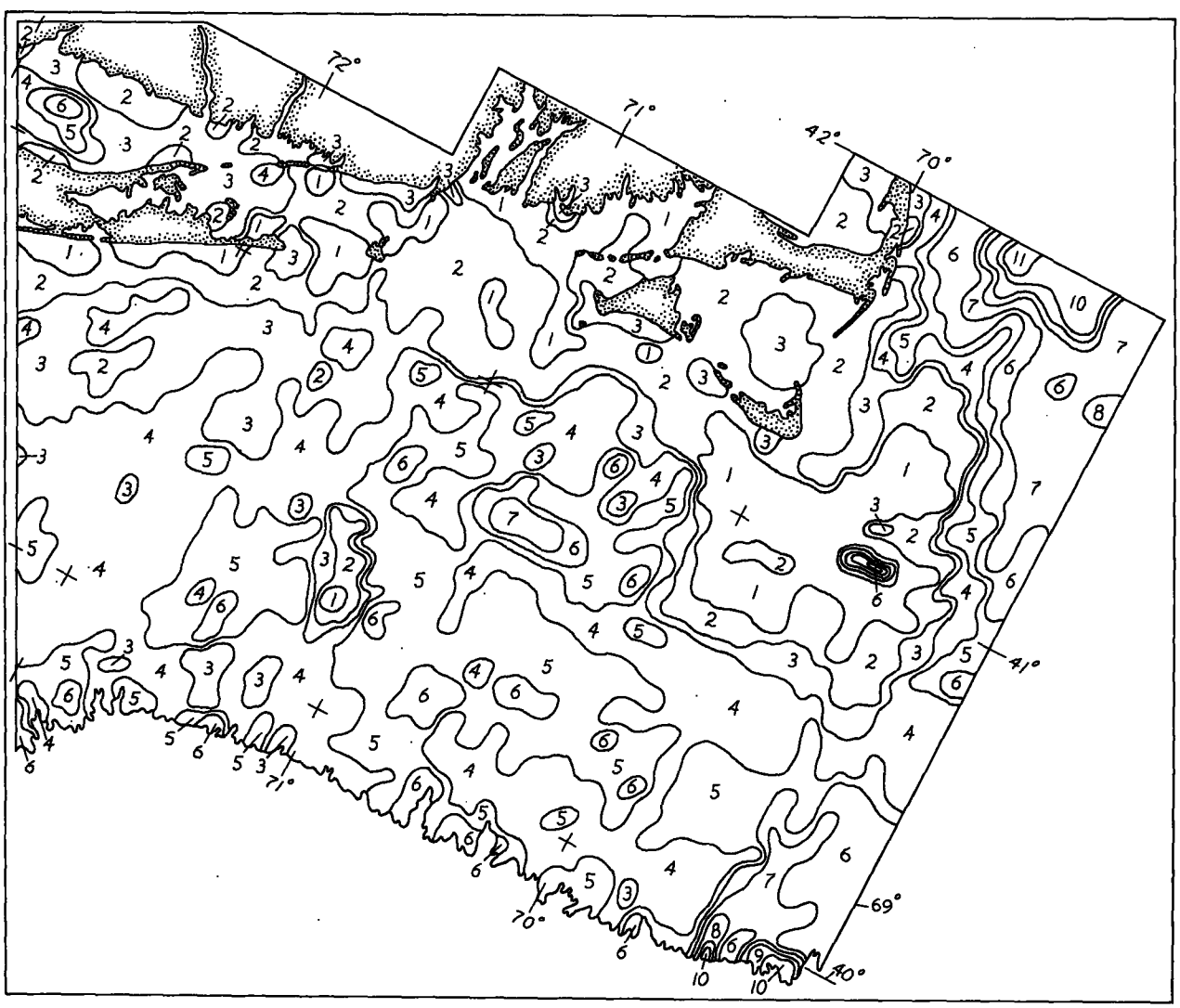
maps are being used aboard a ship, σ must be equated to $\sqrt{\sigma_m^2+\sigma_s^2}$, where σ_m is taken from the position error diagram, and σ_s is computed by dividing the first three terms on the right-hand side of equation 2 by $V_g+\bar{g}^2$, for the area in which the ship is working, and then taking the square root of the quotient.

Distribution of the Map Errors

The standard deviations of the isobath depth error (fig. 2) generally increase in an offshore direction. Most of this increase is due to the steeper topographic slope on the outer shelf and upper slope which makes interpolation of depths between soundings less certain in these regions. A part of the increase is also due to a wider spacing between tracklines offshore.

Most of the large inshore standard deviations are also caused by locally steep topographic slopes (e.g., the Hudson Channel, Long Island Sound, Delaware Bay, and Nantucket Shoals); however, the large deviations east of Cape Cod are due both to wide trackline spacing and to steep slopes.

Figure 4 shows the percentage of the total variance of the depth error which can be attributed to observational, positional, and interpolation errors.



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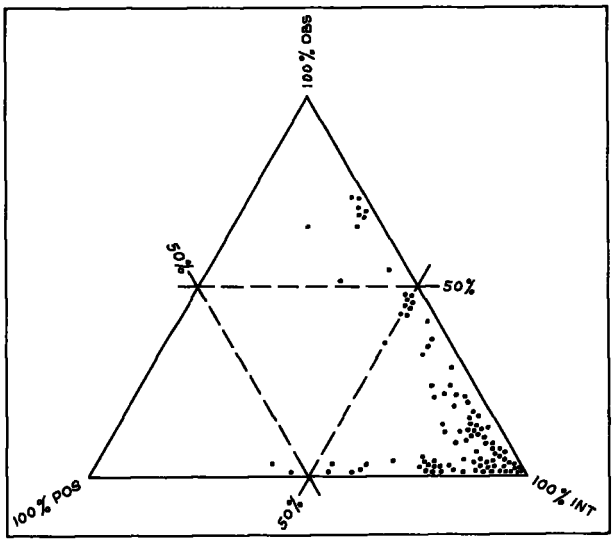

FIGURE 4.—Percentage of the variance of the isobath depth error that can be attributed to observational errors (OBS), positional errors (POS), and interpolation errors (INT).

The figure is based on the variance in 100 representative 5-minute unit areas. In most of these unit areas more than half of the total variance results from uncertainty in interpolations of assumed depths between the original soundings.

Interpolation errors are very sensitive to topographic slope and spacing between soundings. To achieve the same reliability of isobath depths, the spacing of soundings must be much closer in areas of steep slopes than in areas of gentle slopes. For many surveys, not only of bathymetry but of other variables as well, the observations are so widely spaced (usually for reasons of economy) that ordinary positional and observational errors have little effect on the reliability of the final isolines.

Figure 5 shows the relation of the standard deviation of the isobath depth error to the mean topographic slope in a few selected unit areas. The dispersion of the points results largely from variations in the spacing between tracklines.

The standard deviations of the isobath position error (fig. 3) also increase offshore, mostly because of wider spacing between tracklines. Figure 6 shows the relation of these standard deviations to the mean spacing between tracklines. The dispersion of the points is due mainly to variations in the observational and positional errors of the original soundings.

PART 2. GEOMORPHOLOGY

A description of the configuration of the Middle Atlantic Continental Shelf, along with a general discussion of its evolution, of the processes involved in its formation, and of its sediments, is presented in this part of the report.

GENERAL CONSIDERATIONS

The general appearance, geological history, sediment distribution, and geomorphic processes of the Middle Atlantic Shelf are discussed in this section.

General Appearance and Past Geologic History

The present continental border of eastern North America can be divided into five geomorphic zones which roughly parallel the present shoreline (fig. 7): (1) a hilly to mountainous system of parallel valleys and ridges (the Newer, or Folded, Appalachian Mountains), (2) a flat to hilly upland region (the Older Appalachian Mountains), (3) a coastal lowland, in places submerged below present sea-level (the Atlantic Coastal Plain and Continental Shelf), (4) a submerged slope about 1,500 fm. high (the Continental Slope), and (5) a very gently sloping surface merging seaward with the deep ocean floor (the Continental Rise). For a discussion of these geomorphic divisions see Fenneman (1938), Heezan et al. (1959), and Hammond (1964).

Before the Cretaceous Period (some 136 million years ago) a succession of evolving highlands occupied the present sites of the Older Appalachians and the Coastal Plain. According to Dietz and Holden (1966), these highlands were formed when material uplifted from an ancient Continental Slope and Rise and from the adjacent deep-sea floor was added to a then smaller continent. This process of accretion is supposed to have started in the late Ordovician Period (about 445 million years ago) and to have continued until the end of the Permian Period (about 225 million years ago), eventually adding some 150 to 400 or more miles to the continent. (Dates are from Kulp, 1961, and Harland, Smith, and Wilcock, 1964.) The eroded remnants of these old highlands now underlie Cretaceous and younger sediments on the present Coastal Plain; they outcrop in a belt of greatly deformed and altered rocks throughout the Older Appalachian Mountains.

The region west of the Older Appalachians was occupied in pre-Ordovician times by an ancient

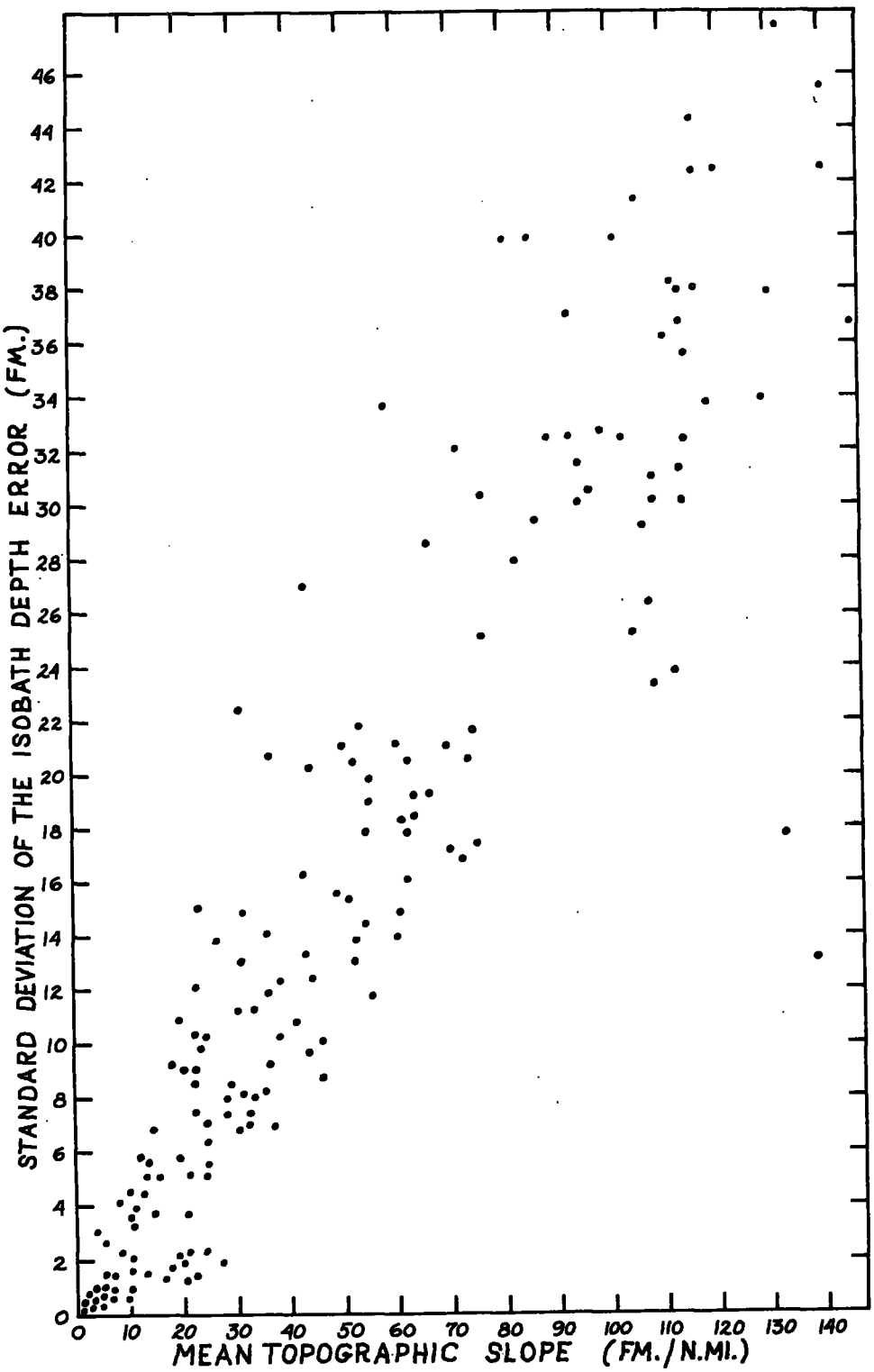

FIGURE 5.—Variation of the standard deviation of the isobath depth error with respect to the mean topographic slope.

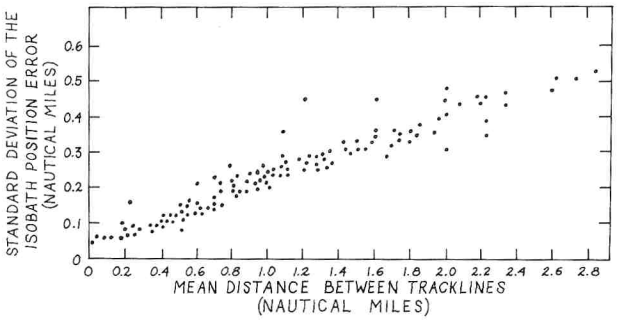

FIGURE 6.—Variation of the standard deviation of the isobath position error with respect to the mean distance between tracklines.

coastal plain and continental shelf. This plain became an epicontinental inland sea in post-Ordovician times, and its bottom was progressively folded until the Appalachian Revolution of middle and late Permian times finally forced it and its sediments into the present Folded Appalachian Mountains. The above sequence of events is only one recent inference from available evidence; for other interpretations of the geologic history of the region see Schuchert (1923), Kay (1951), Drake et al. (1959), Wilson (1966), and Harland (1967); see also the criticism by Hsu (1965) of earlier ideas of Dietz (1963a) and the reply by Dietz (1965).

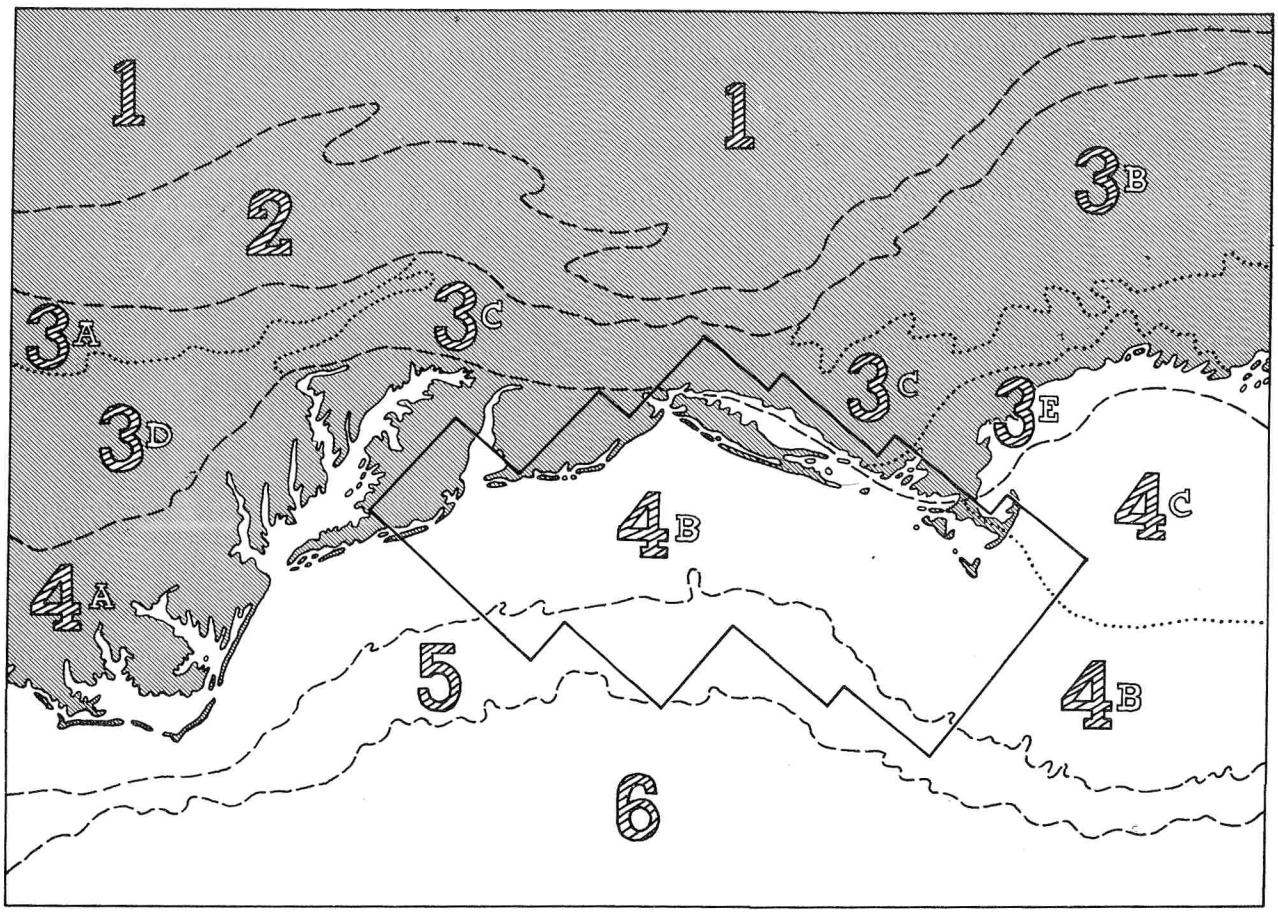

FIGURE 7.—Physiographic regions of the Middle Atlantic Coast. (1) Appalachian Plateaus and Interior Lowlands. (2) Folded Appalachian Mountains. (3) Older Appalachian Mountains, including (3A) Blue Ridge Mountains, (3B) New England-Acadian Mountains, (3C) Piedmont-New England Hills, (3D) Piedmont Plain, and (3E) New England Plain. (4) Emerged and Submerged Coastal Plain, including (4A) Emerged Coastal Plain, (4B) Submerged Coastal Plain or Continental Shelf, and (4C) Gulf of Maine Basin. (5) Continental Slope. (6) Continental Rise. Boundaries are approximate. Sources: Fenneman (1938); Heezen et al. (1959); and Hammond (1964). The heavy solid line is the boundary of the mapped area.

Since the Cretaceous Period, the eroded roots of the old coastal highlands have experienced successive invasions of the sea, and a large wedge of sediment has been deposited on their surfaces. The most recent submergence was between about 4,000 and 20,000 years ago. (For discussions of terrestrial conditions on the shelf in the recent past see Emery, 1966a; Emery, Wigley, and Rubin, 1966; and Wigley, 1966). The presently submerged surface of this sedimentary wedge is the Continental Shelf of eastern North America.

General Sediment Distribution

The surface of the Middle Atlantic Continental Shelf is covered only in part by contemporary sediments. These are mainly in a narrow nearshore zone (Emery, 1961; Uchupi, 1963). The largest part of the shelf is covered by relict deposits formed during lower stands of sea level in the Ice Age.

Relict shelf features and sediments were recognized as early as 1850 by Austen who suggested that the English Channel was once a subaerial river valley. Dana (1863) extended Austen's idea to the Middle Atlantic Continental Shelf by his discovery on an 1852 Coast Survey chart of both the Hudson and Block submarine channels which, he concluded, were once occupied by the Hudson and Connecticut Rivers. Taylor (1872) later suggested that evidence of dry land, rivers, and shoreline features should be found within the 100-fm. line, and during the same period Louis Agassiz taught his Harvard classes that the offshore fishing banks consisted superficially of glacial drift (Upham, 1894). Most recent authors accept the idea of relict deposits, although emphasis shifted somewhat after Gulliver (1899) and Johnson (1919) introduced the concept of an inner shelf which had been cut by waves and an outer shelf which had been built up by wave deposition (for a discussion of this concept see Dietz, 1963b, 1964; and Moore and Curray, 1964).

The Middle Atlantic Shelf is covered by modified glacial outwash and moraines, river channel and flood plain deposits, ancient deltas, offshore bars, and old coastal beach-lagoon complexes (Uchupi, 1968). Some smaller areas may contain materials formed in place by submarine chemical processes (Uchupi, 1963; Emery, 1966b). Superimposed on these primary sediments are patches of both contemporary and ancient shell debris (Merrill, Emery, and Rubin, 1965; Emery, Merrill, and Trumbull, 1965).

The subsurface sediments of the Shelf and Coastal Plain consist of layer after layer of much the same type of deposit that occurs today on their surface (with additions of other types such as peat and limestone). These sediments have been accumulating at least since the Cretaceous Period and now form a thick prism which ranges from a few feet at the landward border of the Coastal Plain to over 15,000 feet (4.6 km.) thick at the edge of the shelf. An even greater thickness has accumulated at the foot of the Continental Slope, and some 25,000 feet (7.6 km.) of sediments now lie under the Continental Rise (for a discussion of this deeper structure see Dietz, 1952; Drake et al., 1959; Heezen et al., 1959; Murray, 1961; Emery, 1966b; Krause, 1966; Hoskins, 1967; and Uchupi and Emery, 1967).

Geomorphic Processes

The nearshore breaking of waves is the most important cause of erosion on the landward edge of the shelf, but is apparently effective only above about 5 to 10 fm. (Dietz, 1963b; see also the discussion by Moore and Curray, 1964 and the answer by Dietz, 1964). Some controversy exists, however, concerning the ability of contemporary processes to alter significantly the relict terrains and sediments seaward of the surf-zone. Several authors have thought that present waves and currents can scour the shelf intensely to great depths (Dana, 1890; Gulliver, 1899; Johnson, 1919; Alexander, 1934; and Jones, 1941). Other workers have suggested that the present shelf surface is drowned and entirely out of adjustment with present conditions (Lindenkohl, 1891; Dietz, 1963b, 1964). Still others have believed that a thin surface layer (6–24 inches, or 15–60 cm.) is in adjustment with contemporary sea level (Donahue, Allen, and Heezen, 1966), or that fine sediments are being either moved across the shelf or deposited in certain restricted areas (Shaler, 1881; Shepard and Cohee, 1936; Stetson, 1938b; and Emery, 1966b). Uchupi (1968) suggested that some linear sand bodies on the inner shelf may have been formed by large modern storm waves. It is also possible that with a long-continued stand of the sea at its present level, the shoreline would build out over a large portion of the inner shelf (Curray, 1964; Emery, 1966b) or that existing bottom sediments

and relict land forms would eventually become completely adjusted to present sea level (Stetson, 1938b, 1939; Moore and Curray, 1964).

A distinction must be made between gross land forms and surficial sediments. All of the relict surface sediments above the late Wisconsin low stand of the sea (about 65 or 70 fm.) have been modified during the last 20,000 years or so by the active surf-zone, as this zone migrated shoreward across the shelf with the latest postglacial (or Holocene) rise of sea level. Thus, the surface sediment layer is a direct product of the Holocene marine transgression. Large terrain features, however, are not likely to have been obliterated by the Holocene rise; hence, much of the present gross morphology on the shelf is probably related to pre-Holocene events.

Between the nearshore surf-zone and the land a complex of barrier beaches, lagoons, and coastal marshes has developed along most of the Middle Atlantic Coast. This complex traps much of the sediment load now brought to the ocean by rivers and other runoff. A large volume of recent sediment is also deposited in bays or sounds, and the small amount of suspended fine material that escapes is often removed from the shelf by currents or deposited in such depressions as the Hudson and Block Channels (Stetson, 1955; Curray, 1964).

As changes have occurred in sea level, the shoreline (along with a complex of barrier beaches, lagoons, coastal marshes, and estuaries) has migrated scores of miles back and forth across what is now the shelf and the emerged coastal plain (Emery, 1967). As early as 1881 Shaler suggested that the net effect of this repeated migration, combined with a slow subsidence of the continental margin, has been the deposition of the series of layers that now form the thick sedimentary wedge of the Continental Shelf.

REGIONAL PHYSIOGRAPHY

The physiographic regions and features on the Middle Atlantic Shelf are described in terms of their topography and sediments in the following paragraphs. The major regions and features discussed are (1) nearshore terrains, (2) terrains southwest of the Hudson Channel, (3) the Hudson Channel, (4) terrains northeast and east of the Hudson Channel, and (5) terraces and ancient shore features on both the inner and outer shelf. The bathymetric maps of Stearns and Garrison (1967) serve as illustrations for this section and should be available; features mentioned in the text are keyed to these maps by chart number. The locations of some of the larger features are also shown in figure 1.

Nearshore Terrains

Nearshore terrains are easily accessible and have been much studied (see, for example, Shaler, 1893, 1895; Johnson, 1919, 1925; Shepard, 1948; and Guilcher, 1958). In the mapped area they may be divided into three types.

The surf-zone.—Parallel to the shoreline is a relatively smooth concave slope, in some places interrupted by one or more offshore bars, extending from the beach to a depth of 5 or 10 fm. The width of the surf-zone rarely exceeds 2 nautical miles (its average width is about one-half mile) and it appears to be deepest off New Jersey and eastern Long Island. The sediments of the surf-zone are mostly clean, coarse to fine sand, with a few patches of gravel and rock. Some black mud that lies between 4 and 11 fm. off New Jersey and Long Island may indicate places where the surf-zone has exposed old coastal marsh deposits such as underlie the present barrier beaches (see Fischer, 1961).

The barrier beach-lagoon complex.—Shoreward of and parallel to the surf-zone, throughout most of the mapped area, are extensive linear barrier beaches forming the seaward margin of shallow bays, lagoons, and coastal marshes. This terrain is especially well developed along the whole of the Maryland, Delaware, New Jersey, and southern Long Island Coasts. The width of the lagoon-coastal marsh terrain usually varies from 1 to 6 nautical miles. Except for tidal channels, the depth of lagoons seldom exceeds 2 fm. and is generally less than 1 fm. The marshes are at sea level, between the high- and low-tide marks; and sediments there are mud and organic plant debris. Tidal-delta sands are around inlets. Barrier beaches are clean sand often formed into sand dunes by the wind (see Lucke, 1934a, 1934b; and Fischer, 1961).

Glacial moraines.—Running across the northern part of the mapped area is a zone of low hills separated from the southern New England shore by a series of bays and sounds. This region of old glacial moraines forms numerous submerged features as well as the backbones of Long Island,

Block Island, and the islands south of Massachusetts (Schafer and Hartshorn, 1965). Long Island has two moraines: the Harbor Hill Moraine extends along the north shore to Orient Point and then across Long Island Sound through Plum, Great Gull, and Fishers Islands to Watch Hill Point in Rhode Island and along the shore (where it is called the Charlestown Moraine) to Point Judith; the Ronkonkoma Moraine runs through central Long Island to Montauk Point. These two moraines are considered to have formed during the last advance of the late Wisconsin ice-sheet some 20,000 years ago (Flint, 1957; and Donner, 1964). They merge to the west, south of Hempstead Harbor, and continue across Brooklyn to Staten Island and New Jersey.

Where the Harbor Hill Moraine crosses Long Island Sound there is a ridge of coarse rocky sediments (chart 0808N–53 of Stearns and Garrison, 1967). Between the high points on this ridge are elongated depressions and channels, some as deep as 55 fm., containing finer sediments. Some of these depressions may be kettles formed by the melting of buried blocks of ice (Elliott et al., 1955), or they may have been cut by either ice-scour or subglacial drainage streams (Dana, 1870, 1875, 1883, 1890; Loring and Nota, 1966, suggested this origin for similar features in the Gulf of St. Lawrence). These pre-Holocene depressions would have become fresh-water lakes shortly after being uncovered by the melting ice-sheet (Antevs, 1922, 1928; Lougee, 1953); evidence for these lakes, in the form of fresh-water clay concretions, has been found in one depression south of Fishers Island (Frankel and Thomas, 1966). Some other depressions may have been formed or at least modified, by river erosion, during the period which followed the retreat of the ice-sheet. All the depressions probably have been scoured by tidal currents which became effective in this area when the sea had risen to 10 to 15 fm. below present sea level.

The Ronkonkoma Moraine extends beyond Long Island, from Montauk Point to Block Island, and its crossing is marked by a broad ridge of coarse rocky and bouldery sediments (charts 0808N–51 and –53). Near its center this band is breached by a channel, which contains several 25- and 30-fm. holes. This breach probably represents one of the ancient channels for the rivers of Connecticut and western Rhode Island. It was later eroded by tidal currents when sea level rose to within 10 or 15 fm. of its present level.

East of Point Judith, R.I., the Harbor Hill (or Charlestown) Moraine appears to bend southward around Narragansett Bay and to join with the Buzzards Bay Moraine of western Cape Cod by way of Browns Ledge and the Elizabeth Islands (chart 0808N–51). This bend is marked by a submerged ridge of coarse gravelly sediments. East of Block Island the Ronkonkoma Moraine also appears to bend to the south and to join with moraines on the north shores of Martha's Vineyard and Nantucket Island by way of Nomans Land, the Southwest Shoal, and Cox Ledge. The bottom in this area is marked by a broad rocky and gravelly ridge (Schafer, 1961; and Kaye, 1964).

Between Block Island and Martha's Vineyard this ridge is breached by a channel with depths as great as 35 fm. The sea bottom between the two moraines in this area contains an east-west channel with depths that approach 30 fm. to the north of Block Island. This east-west channel continues westward through Block Island Sound and eastward as far as the entrance to Vineyard Sound. This channel probably represents an early Holocene drainage system for much of southern New England. Presumably, late Holocene drainage from Connecticut broke through the moraine east of Montauk Point, while Rhode Island and Massachusetts drainage continued down the channel east of Block Island. It appears that both these systems entered the Block Channel across the shelf. The channels have been modified by tidal scour and tidal delta deposition which would have started when the sea rose to about 25 fm. below present sea level.

The moraines on Martha's Vineyard, Nantucket Island, and Cape Cod cannot be traced to the east with certainty (see chart 0708N–51). They probably merge with the lateral moraine of an ice-sheet lobe that once extended southward through the Great South Channel (see Zeigler, Tuttle, Tasha, and Giese, 1964). Between Martha's Vineyard and Nantucket Island is a double tidal delta which appears to have been built in an old tributary of the Block Channel that once ran between the Islands.

Terrains Southwest of the Hudson Channel

Off the coasts of New Jersey, Delaware, and Maryland, the bottom above about 50 fm. consists of alternate ridges and longitudinal depressions, which generally run northeast-southwest and are interspaced by flat areas, escarpments, embayments, and former channels. The sediments on this part of the shelf are predominantly sands with some coarser material. Muds are infrequent above about 50 fm. and are not dominant shallower than the shelf break.

The terrains in this area are similar to present nearshore and modified subaerial alluvial terrains; this similarity is not surprising because the surf-zone, the complex of lagoons and coastal marshes, and the subaerial river regimes must have repeatedly migrated back and forth across the shelf. Flint (1940) noted that north of the James River the Pleistocene formations on the emerged coastal plain are typical of compound alluvial deposits. It seems that this is also true of the submerged shelf, with the addition of numerous transgressive marine features (see also MacClintock, 1943, and Schlee, 1964).

Delaware River channels.—From the mouth of Delaware Bay a channel may be traced southeastward about 40 nautical miles (Lindenkohl, 1891; charts 0807N–56 and –57). Below 20 fm. this channel is lost in a series of what appear to be old lagoons and barrier beaches which continue down to about 40 fm. To the northeast the channel is bounded by a scarp as much as 15 fm. high. A well-defined ridge backing this scarp can be traced 30 nautical miles southeastward from Cape May, and its remnants extend for another 30 or 40 nautical miles.

Northeast of this ridge is a shallow embayment that has a diffuse channel below 5 to 7 fm. (charts 0807N–55 and –56). Deeper than 20 fm. this embayment flattens out and merges with what appears to be a series of lagoons and barrier beaches. Possibly this bay represents an older Delaware River estuary which might be correlated with a post-Sangamon channel in the Cape May Formation on the Cape May Peninsula (Richards, 1962).

Great Egg Harbor River channel.—Running southeast from near Great Egg Harbor Inlet is a smooth embayment that extends to a depth of 12 or 14 fm., where a bar has been built across its mouth (chart 0807N–55). Beyond this bar the bay narrows and a shallow channel continues south-southeastward. Between 18 and 22 fm. a ridge, about 20 nautical miles long, appears to have been a large barrier beach. It encloses what was probably a former lagoon, now as much as 2 or 3 fm. deeper than the surrounding bottom. Below this feature, the channel is lost in a deeper series of what seem to be lagoons and barrier beaches. The northeast boundary of the embayment off Great Egg Harbor Inlet is a low ridge extending southeasterly from Brigantine Shoal; it appears to be composed of a series of submerged sand spits and barrier beaches.

The old and new Delaware embayments and the Great Egg Harbor embayment are each well defined between about 10 and 20 fm. Below about 20 fm., however, the new Delaware embayment is lost, and the old Delaware and Great Egg Harbor embayments are combined, first into a large shallow depression (about 35 nautical miles long) between 24 and 27 fm. and then into a single open embayment between 27 and 29 fm. (charts 0807N–55 and –56). Below about 28 fm., this open embayment narrows into a slender channel which continues southward to about 35 fm., where it is lost in what may be a complex of former lagoons.

The Shelf northeast of Brigantine Shoal.—Northeast of Brigantine Shoal the shelf is dominated by several large northeastward trending embayments, and by two north-south trending channels, which are associated with a submerged alluvial gravel deposit (Schlee, 1964; charts 0807N–54 and –55). One of the north-south trending channels heads offshore near lat. 39°45′ N. and may be traced southward for about 30 nautical miles, roughly along long. 73°50′ W.

West of this channel is a very smooth and flat plain, whose shallow limit is defined by the 10- or 11-fm. isobath. On the east it is bounded by a low scarp and backed by a north-south ridge with a minimum depth of less than 9 fm. This ridge is distinct for at least 35 nautical miles along the bottom, and remnants of it extend even farther both north and south.

East of this ridge is the second of the north-south channels mentioned above. It originates near lat. 39°50′ N. and runs southward for about 30 nautical miles between long. 73°28′ and 73°33′ W. This channel is defined by the 19- to 21-fm. iso-

baths and is extensively barred throughout its length at those depths.

West of this second channel is another plain, somewhat dissected by northeasterly trending depressions; to the east is a broad flat-topped ridge with minimum depths of between 17 and 18 fm. Most of the channels on the east side of this ridge trend northeastward toward the Hudson Channel. North of lat. 39°50′ N., all of the old shelf channels run eastward or northeastward toward the Hudson Channel.

The gravel deposits near these north-south channels seem to have added about 5 fm. to the shelf surface off the coast of northern New Jersey. When compared to the surface south of Long Island this buildup is shown by a greater offshore extent of the 20- to 30-fm. isobaths (compare charts 0807N–54 and 0808N–54 and –55). According to Schlee (1964), these deposits are at least 10,000 years old and were probably deposited by the ancestral Hudson River.

The northernmost and largest of the northeastward trending embayments runs roughly along a line between lat. 39°05′ N., long. 74°04′ W. and lat. 39°24′ N., long. 73°20′ W. (chart 0807N–55). It is well defined between about 20 and 25 fm. and occurs immediately below the submerged gravel deposit described by Schlee (1964). It can be traced for some 50 nautical miles across the shelf and apparently connects with the 37- to 38-fm. depression below Tiger Scarp (chart 0807N–52). Southeast of this largest embayment are four similar but smaller embayments. All of these embayments are bounded on their northwest sides by low scarps and all lead into a north-northeast trending series of apparent lagoons and channels below about 35 fm. To the south these embayments are defined by the 24- to 26-fm. isobaths, but they are progressively less well formed as the end of the Brigantine Shoal Ridge is approached.

The Hudson Channel

The Hudson Channel is the best defined of the old river valleys on the shelf. It was first discovered during the 1842–44 surveys and originally mapped as a series of discrete "mud holes." Dana (1863) later suggested that these holes were part of a continuous valley that had been eroded by the Hudson River. The survey of 1882 demonstrated the continuity of the channel.

The Hudson Channel extends some 85 nautical miles across the shelf from off the entrance to New York Harbor to the head of the Hudson Canyon (charts 0807N–52 and –54, and 0808N–55). It is very shallow at its upper end, but some 10 nautical miles southeast of Sandy Hook it deepens abruptly, runs about 15 nautical miles southward, and then turns southeastward across the shelf. It is divided into a series of basins which are floored with mud and muddy sand. It becomes partially lost in an elongated flood plain and delta below about 40 fm., but several buried channels have been traced through this area, the youngest of which connects to the present head of the Hudson Canyon (Ewing, LePichon, and Ewing, 1963).

According to Ewing et al. (1963), the present Hudson Channel and Delta and the upper slope portion of the Hudson Canyon have all been in much the same position throughout the late Pleistocene. Very likely, however, the present head of the canyon is only one of the latest feeder channels for the lower canyon. Ewing et al. (1963) showed some old buried discontinuities (possibly erosion surfaces) which head northeast of the present canyon. Robertson (1964) suggested that the Georges Bank canyons were eroded during a Pliocene emergence, filled during an upper Pliocene or very early Pleistocene submergence, and then re-excavated during the Pleistocene. Some of the canyons which are immediately northeast of the Hudson Canyon, and which have their present heads below 100 fm. may be of Pliocene age and have not had their heads re-excavated because the Hudson drainage moved out of the area.

Terrains Between the Hudson Channel and the Block Channel

The shelf surface south of Long Island (charts 0808N–53, –54, and –55) has at least three types of relict terrains. Between about 15 and 35 fm. it is characterized by low ridges and shallow channels and appears to be a stream-dissected alluvial plain modified by minor features formed during the Holocene transgression. It is not covered by extensive late Pleistocene alluvial gravels like the shelf southwest of the Hudson Channel.

The shelf surface above about 15 fm. is dominated by Wisconsin glacial outwash and appears as a sand plain in front of the old moraines on Long Island. It has been much modified by early Holocene stream erosion, the late Holocene marine transgression, the modern surf-zone, and possibly

by present-day storm wave action (see discussions of this region by Dana, 1875; Lindenkohl, 1885, 1891; Shepard and Cohee, 1936; Stetson, 1938b, 1949; Lougee, 1953; Elliott et al., 1955; Garrison and McMaster, 1966; and Uchupi, 1968). Below about 35 fm. the surface appears to be dominated by deltaic and alluvial deposition rather than by erosion.

As Garrison and McMaster (1966) pointed out, two major directions of past drainage are apparent on the present shelf surface south of Long Island; one (north of about lat. 40°20′ N.) is eastward into Block Channel, and the other east and southeastward into a large embayment (well defined between about 40 and 45 fm. on charts 0807N–52 and 0808N–54) near lat. 40°00′ N. and long. 72°10–15′ W.

The Block Channel

The Block Channel was discovered during the same surveys of 1842–44 that found the Hudson Channel. This broad and shallow channel extends some 70 nautical miles across the shelf, from inside Block Island Sound to its delta at the shelf break (charts 0807N–51, and 0808N–51 and –52). Block Channel has several minor tributaries entering from the west and two major tributaries entering from the east—one from Rhode Island Sound and Buzzards Bay, and the other from the area south of Nantucket Sound. The Channel and its Rhode Island Sound tributary contain what are apparently well-developed tidal deltas between about 23 and 26 fm.

Dana (1863) suggested that the Block Channel had been eroded by the Connecticut River. Garrison and McMaster (1966) considered it to have been the main trunk for southern New England drainage during late Wisconsin and Holocene times, and Krause (1966) suggested that its delta was forming throughout the Pleistocene. These authors noted that the delta's present form was reached during the early Holocene when sea level was about 45 fm. below the present one. This level is similar to the depth of formation of about 43 fm. proposed by Veatch and Smith (1939) for the Hudson Delta.

Surficial sediments in the Block Channel consist of about 16 inches (41 cm.) of fine fluvial and estuarine sands and silt, probably of Holocene age. These overlie clean medium sands of Wisconsin age and of fluvial origin. The upper 1 inch (2 cm.) or so is sandy silt, with a very high water content; it is probably late Holocene or modern sediment (McMaster and Garrison, 1966; Garrison and McMaster, 1966).

Terrains Between the Block Channel and the Great South Channel

The sea floor east of the Block Channel (exclusive of Nantucket Shoals) is zoned much the same as to the west, although it is very much smoother, contains fewer stream channels and other well-defined offshore features, and is partly covered by considerably different sediments (charts 0807N–51, and 0808N–51 and –52).

Above about 20 fm. the bottom is rough and is composed of Wisconsin glacial outwash and morainal deposits modified by stream erosion, by the late Holocene transgression, and by the present surf-zone. Between about 20 and 35 fm. the shelf is of very low relief and appears to be an alluvial plain modified by a few transgressive features.

The surficial sediments on this plain are fine to coarse sands, which Garrison and McMaster (1966) considered to be pre-Holocene fluvial deposits later reworked by the Holocene transgression. To the east, around the margin of Nantucket Shoals, these authors believed these fluvial sands to be covered by fine sand derived from the Shoals during the late Holocene or present.

The silty region south of Martha's Vineyard.—Below about 30 to 35 fm. evidence of stream erosion is sparse, the bottom is very smooth, and the surface sediments change to sandy silt (chart 0808N–52). This region is unique because it is the only extensive muddy deposit on the entire East Coast Continental Shelf that is not associated with a marked depression. It was first mentioned by Pourtales (1870).

Lindenkohl (1885) considered this muddy area to be a region of Tertiary outcrop that had not been covered by Pleistocene deposits. Shepard and Cohee (1936) thought that the silt was a modern deposit derived from Georges Bank. Stetson (1938b) also thought that silt was now being added to older sand deposits in the area, and Chamberlin and Stearns (1963) have suggested a current eddy to account for this deposition. Garrison and McMaster (1966) noted that the northern edge of the silt deposit is strongly intermixed with older alluvial sands and that the eastern edge appears to

be overlain by younger sand derived from Nantucket Shoals. They believed that the silt accumulated in a topographic depression during the Holocene rise of sea level. Furthermore, they suggested silt beds under Nantucket Shoals as the source and placed the age as late Holocene (after the sea had risen to about 35 fm. below present sea level) because the surface appears smooth and uneroded.

The smooth appearance in this area may be a data artifact, resulting from a rather wide spacing of survey tracklines. Just to the east of the Block Delta is a small well-surveyed area (USCGS Hydrographic Survey No. 6659) that shows the bottom finely dissected by many small channels and covered with a few small mounds and depressions. Although this survey may indicate what the surrounding region would look like if surveyed in comparable detail, there is some doubt that it does.[2] The average standard deviation of the isobath position error in the area of USCGS Hydrographic Survey No. 6659 is 0.13 nautical mile and, because the principal tracklines run parallel to the trend of the small channels (i.e., up and down slope), lengthwise line shifts of one or two times this amount would account for much of the fine detail shown. Some of the crosslines run in this survey, however, give evidence of shallow channels, and it seems probable that the true appearance of the bottom lies somewhere between the two extremes indicated.

Nantucket Shoals.—For a distance of 30 to 50 nautical miles to the south and southeast of Nantucket Island is a vast expanse of sand shoals and a tangle of many smaller ridges and depressions (charts 0708N–51 and –52). Collectively, this area is called Nantucket Shoals and has been known since the earliest explorations of the east coast (see Rich, 1929). Two old maps showing Nantucket Shoals, one made about 1656 and the other about 1730, are reproduced in Gottmann (1961).

From geologic mapping of Nantucket Island, Martha's Vineyard, and Cape Cod, it appears that Nantucket Shoals are relict glacial deposits laid down when the sea was 25 fm. below its present level. The large shoals abutting on the Great South Channel contain a few patches of gravel and probably constitute a much modified glacial moraine formed by a late Wisconsin ice-lobe in that channel. Farther to the west, Nantucket Shoals probably were derived by reworking outwash from the west side of this South Channel moraine, or from an interlobate outwash deposit formed between the South Channel ice-lobe and another ice-lobe extending through Cape Cod Bay (Zeigler et al., 1964, suggested that outer Cape Cod is an interlobate deposit formed between these two lobes), or from end moraines of the Cape Cod Bay ice-lobe. Whatever their exact source, these Shoals have been much altered by early Holocene stream erosion and by late Holocene and modern tidal current and surf-zone action (Lindenkohl, 1883; Curtis, 1913).

Old silt beds occur under the Shoals, and Livingstone (1964) considered them to be of Sangamon age. (Athearn (1957) came to the same conclusion for a similar silt layer about 43 fm. below sea level some 60 nautical miles south of Moriches Bay, Long Island.) Groot and Groot (1964) found that samples of the upper 5 feet (1.5 m.) of the silt near Fishing Rip contained a mixture of Cretaceous, Tertiary, and Pleistocene pollen and spores, as well as a marine shell about 11,500 years old. It, thus, seems that the silt layer, at least near Fishing Rip, has been covered by the Shoal sands only in the late Holocene—probably by material washed southwestward from the lateral moraine of the South Channel ice-lobe. This type of winnowing has been invoked by Garrison and McMaster (1966) to account for the band of fine sand covering the silty area to the west of Nantucket Shoals (see also Shaler, 1893). Uchupi (1968) suggested, however, that some of this sand may have come from the erosion of the outer arm of Cape Cod.

The Great South Channel.—The existence of the Great South Channel was inferred from local surface currents by Captain John Smith as early as 1614 (Rich, 1929). It separates Georges Bank from Nantucket Shoals and is a broad and flat but rough-bottomed valley with a sill at about 40 fm. (lat. 40°36′ N. on chart 0708N–52). It is divided into a number of shallow basins by low sills. This Channel was probably occupied by a lobe of the late-Wisconsin ice-sheet, from which outwash and moraines contributed to both Little Georges Shoal to the east and Nantucket Shoals to the west (see Zeigler et al., 1964). In pre-Pleistocene time Great South Channel may have been a stream valley

[2] Personal communication from John S. Schlee, U.S. Geological Survey, Washington, D.C.

(Johnson and Stolfus, 1924; Shepard, Trefethen, and Cohee, 1934; Emery and Uchupi, 1965; and Uchupi, 1966a, 1966b).

Terraces and Shore Features on the Outer Shelf

Below about 40 fm. the outer shelf is characterized by (1) an alternation of discontinuous scarps and relatively flat terraces, some with superimposed linear ridges of coarse sands and gravels (especially well developed off New Jersey and Delaware) and (2) by ancient river deltas (especially south of New England). Most authors describe the scarps and terraces as old shoreline features, developed during lower Pleistocene sea levels (Taylor, 1872; Newberry, 1878; Lindenkohl, 1891; Shepard, 1932; Stetson, 1938b; Veatch and Smith, 1939; Dietz, 1952; and Emery, 1961).

Old shore lines.—Three sets of terraces with bars and spits are observable throughout the area. The deepest set is between 82 and 90 fm. and averages about 85 fm. Remnants of this set may be seen between Veatch Canyon and Atlantis Canyon (86–90 fm. on chart 0708N–53), just to the east of the head of Block Canyon (82–84 fm. on chart 0807N–51), and to the northeast of Hudson Canyon (82–86 fm. on chart 0807N–52). In addition, Ewing et al. (1963) discovered an 80- to 90-fm. buried erosion surface near the Hudson Canyon (their 165-m. terrace).

A shallower set, from 73 to 81 fm. and averaging about 77 fm., may be seen between Veatch Canyon and Atlantis Canyon (a double set at 78–81 and 73–76 fm. on chart 0708N–53), and to the northeast of Toms Canyon (73–78 fm. on chart 0807N–53). The 85- and 77-fm. sets of terraces south of New England have been combined by Garrison and McMaster (1966) into what they call the 80-fm. terrace.

These terraces are backed by a discontinuous scarp, whose foot is at an average depth of about 77 fm.; this scarp is the Nicholls Shore of Veatch and Smith (1939). It is well defined in the subsurface (Ewing et al., 1963) and, for the most part, appears to be a constructional escarpment formed by younger sediments deposited on an older surface. A more poorly developed deeper scarp, with its foot at about 86 fm., can be seen between Veatch Canyon and Atlantis Canyon (chart 0708N–53), and just to the west of Atlantis Canyon where it merges with the higher Nicholls Shore (chart 0807N–51).

The next set of terraces is between 56 and 71 fm. and averages about 64 fm.; it may be seen between Hydrographer Canyon and Veatch Canyon (59–62 fm. on chart 0708N–53), as well as to the west of Atlantis Canyon (64–70 fm. on chart 0807N–51), and to the northeast of Hudson Canyon (59–62 and 62–70 fm. on chart 0807N–52), Toms Canyon (64–71 fm. on charts 0807N–52 and –53), Wilmington Canyon (56–59 and 63–65 fm. on chart 0807N–56), and Baltimore Canyon (62–66 fm. on chart 0807N–56). Referring to the region south of New England, Garrison and McMaster (1966) called this set the 65-fm. terrace. It is backed by a poorly developed scarp whose foot is at an average depth of about 64 fm. Called the Franklin Shore by Veatch and Smith (1939), this scarp appears to be partly constructional and partly destructional in origin. Ewing et al. (1963) could not find a clear subsurface indication of the Franklin Shore near the Hudson Canyon.

Although these three sets of terraces and scarps were certainly formed when the sea was at various lower levels than at present, it is not easy to determine the exact levels. The difficulty was made plain by Johnson (1910, 1932), Johnson and Winter (1927), and Miller (1939) in discussions of the problems involved in correlating old shorelines now above sea level. These authors concluded that at a given sea-level shoreline features can be developed at different elevations and that determination of former sea levels by physiographic methods alone is, consequently, very inaccurate. Johnson (1932) has also pointed out that a distinction must be made between the elevations of erosional and depositional features formed at the same sea level. All of these conclusions are also applicable to submerged features

Numerous estimates of former sea levels on the outer shelf have been based on appraisals of the eustatic lowering of sea level during the formation of the Pleistocene ice-sheets (e.g., Maclaren, 1842; Taylor, 1872; Shaler, 1875; Daly, 1925; Fairbridge, 1960; Curray, 1961; and Shepard, 1961). Donn, Farrand, and Ewing (1962) give double estimates for this eustatic lowering which correspond with two different estimates of the present thickness of the Antarctic ice-cap. These, combined with dates taken from Emiliani (1961, 1964, 1966) and

Broecker (1966), are: (1) a maximum Illinoian lowering of about 75 or 88 fm. (some 110,000 years ago), (2) a maximum early Wisconsin lowering of about 63 or 74 fm. (some 53,000–60,000 years ago), and (3) a maximum late Wisconsin lowering of about 58 or 68 fm. (some 18,000–20,000 years ago).

In addition to these three terraces, Garrison and McMaster (1966) have noted the existence of another terrace formed when sea level stood at about 45 fm. This level seems to have been the latest episode in (1) large delta formation, especially south of New England, and (2) extensive barrier beach-lagoon formation off New Jersey and Delaware. The 45-fm. terrace is well developed near the Block Delta, where there is also evidence of small lagoons to the east (chart 0808N–52), and of a large spit and a barrier beach-lagoon complex to the west (charts 0807N–51 and 0808N–54). The terrace is also well developed between the Block Delta and the Hudson Canyon (chart 0807N–52) and between Toms and Wilmington Canyons where a large embayment and an extensive series of barrier beaches and lagoons seem to have formed (chart 0807N–53).

Deltas.—Old river deltas along the 45-fm. terrace are especially well developed northeast of the Hudson Channel. The 45-fm. level was the most recent episode in a long history of large-scale deltaic deposition on this part of the outer shelf. The most typical and best preserved of the old deltas is associated with Block Channel (Garrison and McMaster, 1966). From seismic profiles Krause (1966) has concluded that this delta probably existed throughout the Pleistocene. Where it bulges out over the edge of the shelf and onto the upper Continental Slope, Krause's profiles revealed a large area of bottomset beds.

Between the Block and Hudson Deltas a small delta is associated with the southeasterly drainage pattern south of Long Island. Probably of late Wisconsin or Holocene age, this delta appears to lie almost completely above the 64-fm. terrace northeast of the Hudson Canyon (chart 0807N–52).

The Hudson Channel disappears below about 40 fm. in what Veatch and Smith (1939) have called the Hudson Apron, a large delta whose latest stage of construction occurred when sea level stood at about 43 fm. The large bar, or spit, just to the northeast of the Hudson Canyon, may represent the remains of an earlier delta built during or shortly after the late Wisconsin maximum sea level regression (which probably formed the 64-fm. surface under this feature). Similar large spits to the northeast of both Wilmington and Baltimore Canyons (chart 0807N–56) may also be remnants of early or late Wisconsin deltas—probably built in this area by the Delaware River. Little evidence exists of delta formation at the 45-fm. level east of Block Channel.

Canyons and the slope complex.—The Continental Slope of Eastern North America was discovered in the early 19th century, but it was not studied in detail until the 1870's, when the first successful wire-sounding machines were introduced. The Coast Survey steamer *Blake* surveyed the slope during 1877–80 (Agassiz, 1888), and the Fish Commission steamers *Fish Hawk* and *Albatross* did extensive deep-water biological dredging, especially south of New England, during the 1880's.

Although the upper parts of canyons on the edge of the Scotian Shelf and Grand Banks had long been known to commercial fishermen (see Collins, 1885, and Johnson, 1885), no evidence of Middle Atlantic canyons was obtained until the 1842 work of the Coast Survey. After the soundings from the 1842 surveys were plotted, nautical charts carried notations of a "145-fathom hole" near the head of Hudson Canyon. Dana (1863) used an 1852 chart to trace the Hudson and Block Channels across the Shelf, but the new surveys of 1882 were required to show the immense size of the Hudson Canyon and its extension to the bottom of the Continental Slope (Lindenkohl, 1885). The upper part of another canyon, later named the Atlantis Canyon, was discovered by the *Albatross* in 1884 (Tanner, 1886). After the discoveries of the 1880's the canyons were much discussed (see Upham 1890a, 1890b, 1894; and Spencer, 1890, 1903, 1905a, 1905b)—usually in attempts to support theories of a vast uplift of the North American continent during the late Tertiary or early Pleistocene, which was supposed to have caused the ice age—but little new field work was done until the surveys by the USCGS in the 1930's (discussed by Shepard, 1931, 1933a, 1933b, 1934, 1938; Daly, 1936; Shepard and Beard, 1938; and Stetson, 1938a, 1938c). This work culminated in the report and charts of Veatch and

Smith (1939)—see also Smith (1939, 1940a, 1940b, 1941).

The origin of these canyons is still an open question, but most recent authors believe that they were formed by a combination of fluvial processes delivering sediment during lower stands of the sea and submarine transport of the sediment by mass movement and turbidity currents seaward of the shelf. Review articles on the canyons as well as on the Continental Slope and Rise have been made by Johnson (1938–1939, 1939), Veatch and Smith (1939), Stetson (1949), Deitz and Menard (1951), Dietz (1952, 1963a), Kuenen (1953), Drake et al. (1959), Heezen et al. (1959), Shepard (1963), Guilcher (1963a, 1963b), Heezen (1963), Moore and Curray (1963), Hoskins and Hersey (1965), Emery (1966b), Krause (1966), and Heezen, Hollister, and Ruddiman (1966).

The surface sediments of the slope and canyons consist of rock outcrops, deltaic deposits, and slumping debris, all of which are more or less covered by a veneer of late Pleistocene and present-day muds and organic oozes.

Terraces and Shore Features on the Inner Shelf

For the most part the inner shelf is made up of alluvial plains that have been modified by glacial outwash and by the Holocene transgression. Much of this has been discussed in preceding sections, but some of the better defined features deserve further mention. Although transgressive features occur on the inner shelf at almost every level between the present shore and about 40 fm., they seem to be concentrated in at least four major bands that occur at about 6 to 15, 15 to 27, 28 to 33, and 33 to 40 fm.

The shallowest of these bands (6–15 fm.) has been described by McMaster and Garrison (1967) who noted evidence of a barrier spit and lagoon south of Block Island at about 13 fm. (chart 0808N–51). Similar spits can also be found at about 13 fm. southeast of Cape May (chart 0807N–56), across the Great Egg Harbor River Channel and east of Brigantine Shoal (chart 0807N–55), southeast of Montauk Point (chart 0808N–53), east of Point Judith and south of Nomans Land (chart 0808N–51). Furthermore, Elliott et al. (1955) have noted a ridge, which crosses the Delaware Channel at a depth of about 15 fm., and have suggested that this ridge may be the remains of a submerged coastal terrace (chart 0807N–57).

The 6- to 15-fm. band is also well represented by channel bars and small depressions off the coasts of Delaware and New Jersey, by the barred terrace below Cholera Bank south of western Long Island (chart 0808N–55), by the tidal delta between Martha's Vineyard and Nantucket Island (chart 0808N–51), and by the higher parts of Nantucket Shoals. Most of these features are probably of late Holocene age.

The second band (15–27 fm.) is represented by: many apparent channel bars, barrier beaches, and lagoons off the coasts of Delaware and southern New Jersey; by spits and bars above Tiger Scarp (chart 0807N–52); by Cox Ledge south of Narragansett Bay and the tidal deltas in the Block Channel system (chart 0808N–51); and by a platform with numerous sand ridges south of the southeastern part of Nantucket Shoals (chart 0708N–52). These features are probably of Holocene age, with the possible exception of the platform south of Nantucket Shoals. This platform may represent the old silt beds under the Shoals and may be as old as the Sangamon (Livingstone, 1964); however, its covering of sand ridges is probably Holocene (Groot and Groot, 1964).

A Holocene age estimate for the features in this band is supported by the discovery of fossil oysters, *Crassostrea virginica*, some with radiocarbon ages of 7,300 to 10,300 years, at depths of 18 to 24 fm. throughout the mapped area (Merrill et al., 1965; Emery and Garrison, 1967). Living oysters of this species are found almost entirely in shallow inshore waters. Old fresh-water peat deposits, with radiocarbon ages of 8,600 to 11,000 years, have also been found in this band on Nantucket Shoals (Emery, Wigley, Bartlett, Rubin, and Barghoorn, 1967).

The third band (28–33 fm.) is represented by bars and lagoons off southern New Jersey and by barred terraces south of Long Island and Massachusetts. These features are also probably of Holocene age. Fossil oysters, some with radiocarbon ages of 9,800 to 10,800 years, have been found concentrated in this band throughout the area (Merrill et al., 1965; Emery and Garrison, 1967). An old peat deposit has been found at a depth of about 32 fm. on Georges Bank, just to the east of the region discussed in the present report; this has a

radiocarbon age of about 11,000 years (Emery et al., 1966, 1967).

The fourth band (33–40 fm.) is marked by several terrace remnants, some with extensive bars and lagoons. For example, the foot of Fortune Scarp (northeast of the Hudson Delta) lies at about 37 to 38 fm. and the foot of Tiger Scarp at about 33 to 36 fm. (chart 0807N–52). Garrison and McMaster (1966) also noted that a significant percentage of what appear to be Holocene ridge tops south of New England are at depths of 34 to 39 fm. and an old fresh-water peat deposit has been discovered at 36 fm. just south of the mapped region (Emery et al., 1967). This peat has a radiocarbon age of 13,500 years.

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FEEDING RATES OF STARFISH, *ASTERIAS FORBESI* (DESOR), AT CONTROLLED WATER TEMPERATURES AND DURING DIFFERENT SEASONS OF THE YEAR

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ABSTRACT

Starfish were held for 28 days in pans with running sea water maintained at a series of constant temperatures, with oysters as food. The average number of oysters eaten per starfish during this period was 2.3 at 5° C., 3.0 at 10° C., 4.1 at 15° C., 5.0 at 20° C., 2.8 at 22.5° C., and 1.0 at 25° C. Starfish lost weight at 25° C. To observe seasonal feeding rates, starfish and oysters were held in trays suspended in Milford Harbor, Conn. Starfish fed little from mid-January to the end of March, but the rate of feeding then increased rapidly to a maximum in late June and early July. After mid-July, starfish fed at about one-third the rate of late June. This second period of low feeding, which appeared to be associated with both high temperatures and spawning, lasted from July through September. From late October through early December the rate of feeding increased again to about two-thirds of the level in late June and early July, before decreasing again to the seasonal low in mid-January.

Information in the literature on feeding rates of starfish, *Asterias forbesi* (Desor), is limited, and no one has reported studies of feeding rates at different specific temperatures maintained within closely controlled limits. In addition, no one has reported quantitative studies that describe possible changes in feeding rates during different seasons of the year. Although Galtsoff and Loosanoff (1939) stated that starfish in Long Island Sound feed more actively during the summer than during the winter, they did not determine specific rates. Needler (1941) reported that *Asterias vulgaris* (Verrill) in waters of Eastern Canada feed mostly in the spring and fall and relatively little in the winter. (In both Long Island Sound and Eastern Canada, water temperatures fall to slightly below 0° C. in the winter.) According to Hancock (1955, 1958), *Asterias rubens L.*, which inhabit English waters, feed at a high rate throughout the winter. Near Essex, England, where the studies were made, water temperatures average 4° to 8° C. during the winter. He reported that the only important seasonal lull occurs just after the spawning season in May and that feeding increases again sometime between September and November. Because he made no controlled laboratory studies of feeding rates at a series of constant temperatures, he could not determine whether the decline in feeding after May was in response to high water temperatures, which rose above 15° C., or to spawning. Thorson (1955) found that the brittle star, *Amphiura* sp., does not feed for 1 month before spawning in late summer; after spawning it lies quiescent on the bottom, not feeding for about another month.

I have attempted to determine feeding rates of starfish at a series of constant temperatures and during different seasons of the year. In the study of seasonal feeding, I wanted especially to obtain a record of possible feeding during winter and to determine whether feeding slows down in midsummer after starfish begin to spawn. Spawning of starfish in Long Island Sound begins in the middle of June and continues intermittently through the summer (Galtsoff and Loosanoff, 1939; Loosanoff, 1961). During the experiments I also recorded the gains and losses in weight of starfish. I believed that such a study would provide important data on the biology of starfish and useful information for commercial growers of shellfish.

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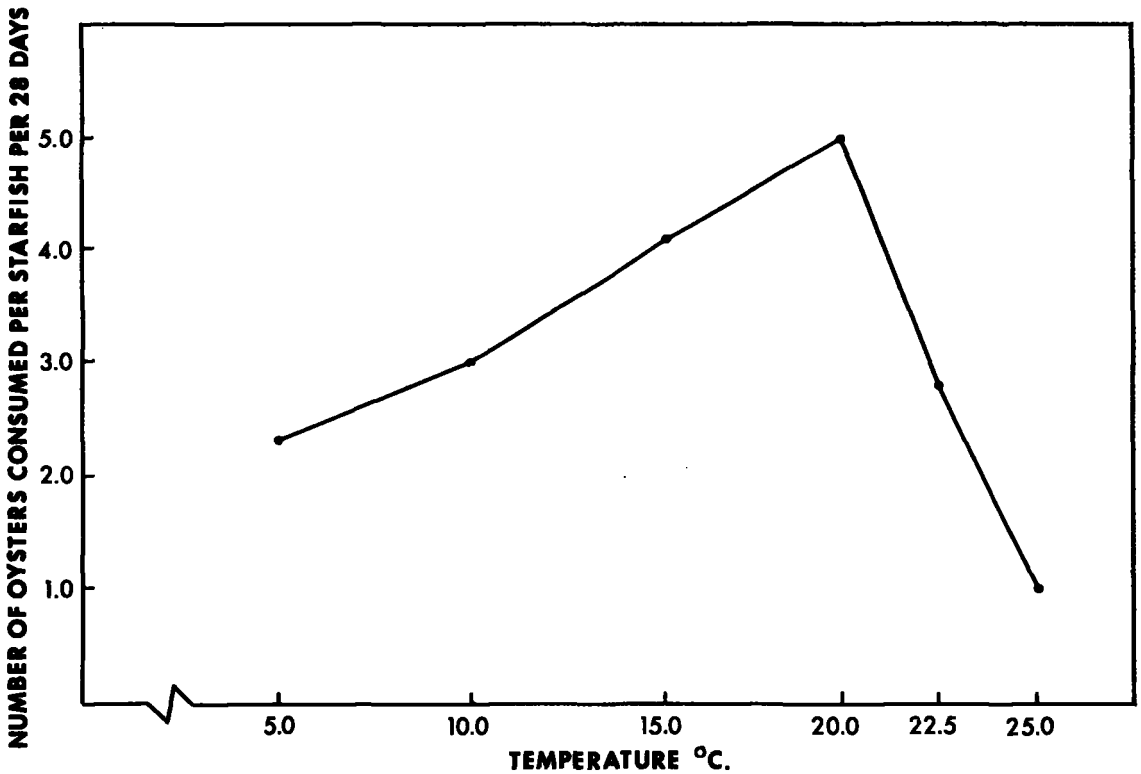

FIGURE 1.—Feeding rates of starfish on oysters at constant temperatures. (Points are based on combined data of replicates at each temperature level—see table 1.)

FEEDING RATES AT CONSTANT TEMPERATURES

METHODS

For the feeding experiments with starfish held at constant temperatures, wooden frames, constructed to hold a bank of four enamel trays (6 cm. by 43 cm. by 50.5 cm.), were arranged on laboratory tables. Each bank was supplied with a separate, continuous flow of sea water. By mixing cold and heated sea water in glass cylinders just above the frames, we maintained the water in the trays within ±1° C. of the temperature desired.

I believe the range of salinity of the water (26.8‰–28.2‰), which corresponds with that of the natural habitat of starfish near Milford, Conn., did not significantly influence the feeding rates during the experiment.

At each temperature four or eight trays were used, each containing 3 adult starfish and 40 oysters. The starfish weighed between 39 and 41 g. (starfish were drained individually for 30 seconds before weighing) and averaged 64 mm. (range 53–75 mm.) from tip of two arms nearest the madreporite to the madreporite. The heights of the oysters averaged about 50 mm. (range 34–80 mm.). Some oysters were in clusters, and others were individuals. To ensure an ample food supply for the starfish, shells of consumed oysters were removed nearly every day and replaced by live oysters.

A fresh group of starfish was obtained in Long Island Sound off Milford for each repetition of a 28-day test at a series of temperatures. These animals were placed in large containers of water at the same temperatures as when they were collected. As the water temperature gradually rose indoors to the point desired, starfish were placed in the experimental feeding trays maintained at this temperature. Oysters, acclimated to the experimental temperature in the same way, were placed in trays with the starfish 1 or 2 days later. Only one starfish died in pans in which water temperatures ranged from 5° to 22.5° C. At 25° C., however, 14 of 72 starfish died during the experiments and one additional starfish lost an arm.

RESULTS

Feeding rates are expressed as the number of oysters consumed per starfish during the 28 days

of feeding. Only one test was made at 5° C. (because low temperatures could not be maintained during late spring); three each at 10° C., 15° C., and 20° C.; one at 22.5° C.; and four at 25° C. Results obtained during replicate tests at the same temperature were similar (table 1).

The rate of feeding was strongly influenced by the temperature of the water. At 5° C. starfish consumed an average of 2.3 oysters each during the 28-day period. The rate of feeding increased by about 1 oyster for each 5° C. increase to 20° C.—to 3.0 oysters per starfish at 10° C., 4.1 at 15° C., and 5.0 at 20° C.; it then decreased to 2.8 at 22.5° C. and 1.0 at 25° C. (fig. 1). Thus, the optimum temperature for feeding of starfish on oysters was 20° C.

Additional observations showed that frequently two starfish and sometimes all three in a pan fed simultaneously on the same oyster or group of oysters in a cluster. Starfish did not always consume all the tissues of oysters they killed; a small amount often remained near the hinge of the oyster after a starfish had left it.

TABLE 1.—*Feeding rates of* A. forbesi *on oysters, height about 50 mm. (range 34–80 mm.), at a series of controlled water temperatures. Rates are given as the average number of oysters consumed per starfish in 28 days*

Temperature and test number	Starfish used in test	Oysters consumed	
		Total	Per starfish
5.0° C.	*Number*	*Number*	*Number*
1	12	27	2.3
10.0° C.			
1	12	35	2.9
2	12	32	2.7
3	24	78	3.2
15.0° C.			
1	12	57	4.7
2	12	47	3.9
3	24	94	3.9
20.0° C.			
1	12	62	5.2
2	24	116	4.8
3	24	120	5.0
22.5° C.			
1	24	67	2.8
25.0° C.			
1	12	18	1.5
2	12	13	1.1
3	24	29	1.2
4	24	12	.5

Besides observing feeding rates of starfish, I measured changes in their weight during 28-day test periods. Average gains in weight were 4.4 g. at 5° C., 7.1 g. at 10° C., 13 g. at 15° C., 13.7 g. at 20° C., and 5.8 g. at 22.5° C. At 25° C. starfish lost an average of 6.5 g. (fig. 2).

The loss in weight by starfish held at 25° C., even though they consumed food, shows that if starfish were held at this temperature for an extended period of time, they would probably die. In figure 2 the line connecting the number of grams gained or lost by starfish supplied with food crosses the point where no weight is gained or lost at about 23.5° C. It would seem, therefore, that starfish from Long Island Sound would probably die if they were maintained for a long period at temperatures above 23.5° C.

As controls in the weight studies, starfish were held in three different situations without food. Nine starfish held in a laboratory tray without food for 28 days at 15° C. lost an average of 7.1 g., and 12 held at 25° C. lost an average of 8.6 g. (fig. 2). Twelve starfish held in a small plastic screen cage in Milford Harbor from April 1 to 30, 1965, when the temperature averaged 5.8° C. (range 2.7–9.5° C.), lost an average of 3.2 g.

FEEDING RATES DURING DIFFERENT SEASONS

METHODS

To study feeding rates during different seasons, trays, measuring 14 cm. by 83 cm. by 147 cm., were suspended from the laboratory dock in Milford Harbor. They were covered and lined on the inside with plastic screening (mesh size 3 holes to the cm.). Depths of water over the trays ranged from 0.75 m. at low tide to 2.5 m. at high tide. Each tray held 20 adult starfish and 140 oysters. From January 20, 1964 to January 26, 1967, one tray was examined once every 2 to 4 weeks. An examination consisted of lifting the tray out of water, placing the starfish in buckets of water, washing the tray with a hose, counting the oysters consumed by starfish, replacing them with live oysters of the same size, returning the starfish to the tray, and then lowering the tray to its normal position.

From May 17, 1966 to January 26, 1967, a period of slightly more than 8 months, a second tray similar to the first was examined in the same manner on each date, except that after each examination the starfish and oysters were transferred to a clean replacement tray. This procedure was followed to ensure that starfish were not consuming large fouling organisms, which might have set in the tray, rather than the added oysters, thereby giving a false indication of their rate of feeding.

RESULTS

Starfish in trays suspended in Milford Harbor displayed the same pattern of feeding in each of the 3 years of observations (fig. 3). The rate of

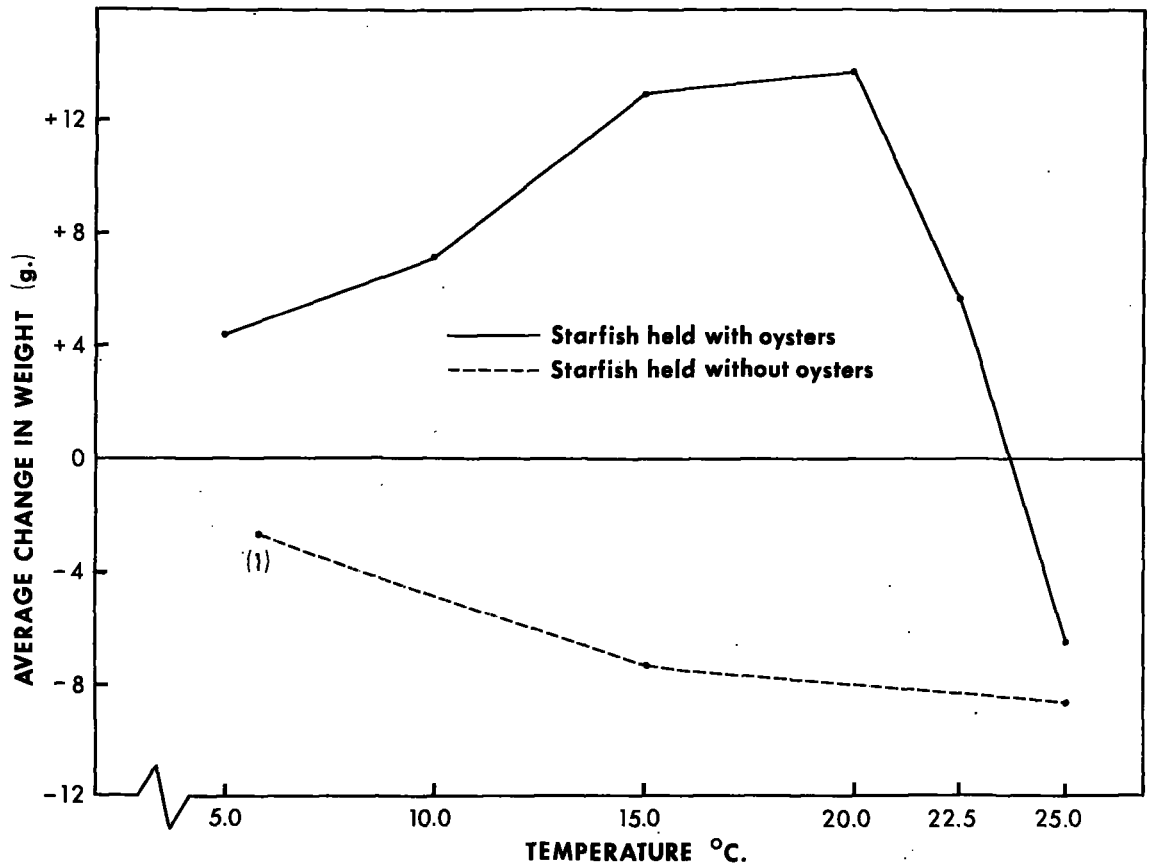

FIGURE 2.—Average weight change of starfish held at constant temperatures for 28 days, with and without food. (Points are based on combined data of replicates at each temperature.) Point (1) represents starfish held in a cage in Milford Harbor, April 1–30, when temperatures averaged 5.8° C. (range 2.7–9.5° C.).

feeding was low from mid-January until the end of March. For example, in 1965 the 20 starfish consumed about 0.6 oyster per 7 days (0.12 oyster per starfish per 28 days) during this period of 2.5 months. From mid-April to late June and early July the rate rose sharply, apparently as a result of the rise in water temperature. At the time of most intense feeding, in late June 1965, the 20 starfish ate about 20 oysters per 7 days (four oysters per starfish per 28 days). In late July, August, and September the rate of feeding decreased to about a third of its level in late June and early July. In late October, November, and early December the rate increased again to about two-thirds of the rate in late June and early July. Beginning in late December, feeding rates began to decline but did not really become low in 1965 and 1966 until mid-January. In 1967, however, because of unusually warm water, feeding had not declined to its previous winter low by late January when observations were terminated.

As the experiment continued from 1964 through 1966, the starfish grew larger. The new group of oysters collected each spring was, however, of about the same average size—50 to 65 mm. (range 34–82 mm.)—as the original group fed to the starfish in 1964. Because the larger starfish consumed more oysters (of a particular size) than the smaller ones, feeding rates were higher in each successive year.

The feeding in the second tray, observed from May 17, 1966 to January 26, 1967 (to evaluate the effect of possible consumption of fouling organisms on feeding rate), was essentially similar to that in the first tray. Because the supply of oysters was low, however, it was necessary to use smaller oysters in this tray after late August. The starfish in this second tray, consequently, showed a much higher consumption of oysters than did those in the first tray which were feeding on larger oysters (fig. 3).

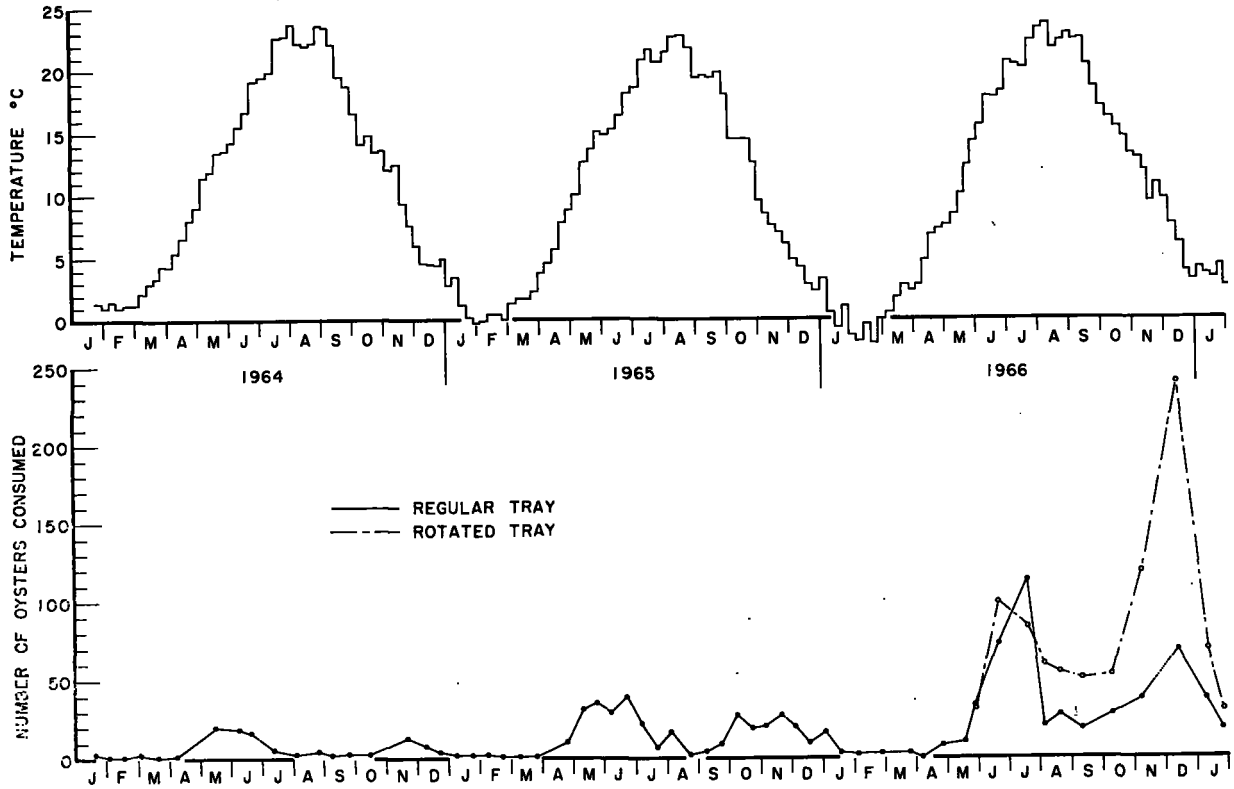

FIGURE 3.—Number of oysters consumed by 20 adult starfish held with 140 oysters in a tray from January 1964 to January 1967 and (in a second tray) from May 1966 to January 1967. Both trays were suspended in Milford Harbor. Temperatures are given in the upper panel.

In 1964, 1965, and 1966, during the period of little feeding from mid-January to the end of March, water temperatures averaged 1° C. (range −2.2° to 3.2° C.). Observations of starfish in trays in Milford Harbor and of those dredged from the bottom showed that they feed on oysters and other food at temperatures at least as low as 0.2° C. Temperatures increased to 7° to 9° C. by the end of April, to 13.5° to 15° C. by the end of May, and to 18.5° to 19.5° C. by the end of June (when the rates of feeding were highest). By mid-to-late July temperatures reached 22.5° C. and stayed at or above that level until early or mid-September (during the period when rates of feeding were about a third as intense as they were in the spring). In the 3 years temperatures averaged 13.5° to 15.3° C. during October, 7.9° to 11.6° C. during November, and 3.6° to 5.8° C. during December, and during this period of 3 months feeding rates were about two-thirds as intense as they were in late June.

SUMMARY OF EFFECTS OF WATER TEMPERATURES AND SEASONS ON FEEDING RATE

A comparison of feeding rates of starfish at constant temperatures with those in different seasons shows that the rates in different seasons are controlled primarily by seasonal temperatures. Though laboratory studies were not conducted to determine feeding rates at temperatures below 5° C., low rates from mid-January to the end of March are undoubtedly a result of temperatures which average only 1° C. As temperatures rise in the spring to nearly 20° C., the optimum temperature for feeding, by the end of June feeding increases rapidly.

In summer the decline in feeding coincided with high temperatures. For example, in 1964 temperatures exceeded 22.5° C., the temperature at which feeding probably begins to decline, on July 15, about 2 weeks after a sharp decline in feeding had already begun. In 1965 temperatures rose to above 22.5° C. for only a few days during July, coincid-

ing with the decline in feeding. In 1966 temperatures rose above 22.5° C. on July 7 shortly before feeding declined. In 1964, because feeding began to slow down before temperatures reached 22.5° C. and continued low in late September and early October after temperatures dropped well below 22.5° C., some other factor—probably the effects of spawning which started in mid-June—seemed to be partly responsible for the low feeding rate. In 1965, the possible effects of spawning were observed through September because feeding was low even though temperatures were 16° to 21° C. In 1966, low feeding was recorded from mid-September through early October when temperatures ranged from 16° to 22.5° C. The rate of feeding increased again in late October and remained high through most of November as temperatures dropped to 15° C. and lower. Feeding rates declined in late December when temperatures fell to 2° to 4° C. and reached the winter low by mid-January when the temperature fell to about 1° C.

Asterias forbesi in Long Island Sound exhibits a reduction in feeding in midsummer similar to that reported by Needler (1941) for *A. vulgaris* in Eastern Canada and by Hancock (1955, 1958) for *A. rubens* in English waters. In contrast to *Amphiura* sp., as described by Thorson (1955), *A. forbesi* apparently feeds actively right up to the time it spawns.

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Barry Baiardi, Russell Clark, and Otis Lane provided technical assistance, and Herman R. Glas collected starfish.

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FACTORS INFLUENCING THE ATTRACTION OF ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS*, TO ARTIFICIAL LIGHTS

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ABSTRACT

Using artificial lights to attract fish at night is a common and often effective fishing technique. With Atlantic herring the attraction is somewhat uncertain, however, and does not always take place. This paper describes experiments which showed that, in addition to the inherent variability of the fish themselves, certain external conditions can modify the attraction to the light. Attraction was greater at low than at high temperatures, greater with underwater lights than with lights above the surface, and greater when the fish were previously adapted to light than when they were adapted to darkness. Very bright light (illumination 20–600 lux), especially above the surface, tended to repel the fish. Light of intermediate intensity (illumination 1–30 lux) was most effective.

The behavioral responses comprised an initial attraction resembling positive phototaxis, followed by apparent disorientation, or confusion. The disorientation may have been due to attempts by the fish to respond with a dorsal light reaction, i.e. to assume postures which would orient their dorsal surface toward the light source even when such postures interfered with normal swimming.

The use of artificial lights for attracting fish is a common practice in fisheries throughout the world. The methods have changed but little, however, the chief improvement being the substitution of electric light sources for open flames or fuel-burning lamps.

The attraction of Atlantic herring (*Clupea harengus harengus*) with lights has been studied experimentally and adapted to some extent for commercial fishing. Lights have been used routinely on Norwegian purse seiners for many years to attract herring. According to Dragesund (1958), herring are not always attracted to lights, however, and even the fishermen do not agree about the behavior of herring in response to the lights used on seiners. Dragesund studied the behavior of fish schools from a research vessel and distinguished the following kinds of reaction to the attracting light:

1. Fish descend and pack together.
2. Fish disperse.
3. Fish rise toward light, then shortly descend.
4. Fish pack together, then rise toward the light.

Blaxter and Parrish (1958) were able to attract young herring (5–25 cm.) to underwater lights at several levels of brightness and to bring them to the surface by raising the lights. Tibbo (1965) reported that herring in a large tank were attracted to artificial lights of various intensities and colors, although they were repelled at the highest intensities. Gauthier (in press), collaborating with fishermen on a commercial purse seiner, reported catches of herring of 25 to 40 tons in trials with underwater lights in the Gulf of St. Lawrence.

Lights were used traditionally along the Atlantic Coast of North America for catching juvenile herring by "torching," a method probably adopted from the Indians. A kerosene- or gasoline-burning flare, or even a more primitive torch of combustible material on a stick, was mounted on the bow of a small boat. The procedure has been described by Earll (1887) as follows. "The fishermen usually go to the shore late in the afternoon and time their departure so as to reach the fishing grounds shortly after sunset. As soon as it becomes sufficiently dark, the fire is lighted, one man takes his position in the stern to steer the boat and another stations himself in the bow, armed with a dip-net for securing the fish as they gather in little bunches just in front of the light. The remaining members of the crew row the boat rapidly through the water, while the man in the bow is busily engaged in throwing the fish into the boat

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by means of his dip-net. Great numbers of herring are attracted by the light and it is not uncommon for fifteen or twenty barrels to be taken in a few hours."

The variability of the herring's response to light is a characteristic feature and has been noted by many investigators. Blaxter and Holliday (1963) stated ". . . . Such reactions will vary widely depending on the environment and the physiological state and age of the fish as well as on the type of stimulus itself." Other authors have demonstrated how many factors, external and internal, can vary the response of herring and other species to artificial lights. Kurc (in press) and others have pointed out how the thermocline may prevent fish from rising to a light, or may hold them in the surface water so that they can be more readily attracted. Strong ambient light (e.g. moonlight) may reduce the effectiveness of the attracting light (Kurc, in press; Ström, in press). Woodhead (1956) showed that starvation reversed the normal negative phototaxis of the minnow *Phoxinus*. Andrews (1946) found that the attraction to light of the white sucker (*Catastomus*) decreased with increasing temperature. Sudden changes in illumination may cause the fish to disperse instead of attracting them (Ström, in press; Gauthier, in press).

Although routine, uncritical use of lights to attract fish may sometimes be successful, far greater effectiveness might be achieved by a better understanding of the underlying behavior of the fish and its response to lights. Moreover, lights might be of definite value in some circumstances where they are not now used. In Maine the use of lights for catching herring is generally illegal because many fishermen believe that the lights tend to disperse the herring rather than attract them (Scattergood and Tibbo, 1959). This restriction appears to be an instance where profitable use of lights has been discouraged because the underlying behavior of the fish has been inadequately understood.

This paper is an attempt to explain some of the biological and other factors that are conducive to the attraction of herring by light.

METHODS

The fish used in the experiments were immature Atlantic herring of age groups O (brit), I, and II, which are processed as Maine sardines. They were 75 to 200 mm. in total length and were taken from commercial catches near Boothbay Harbor, Maine. The fish were held under the prevailing seasonal conditions of salinity, temperature, and dissolved oxygen in large tanks provided with running sea water and were fed daily a mixture of ground trout food and canned cat food.

The experiments were conducted in a separate tank. This tank was fiberglass, 5.5 m. long, 0.4 m. deep, and 0.3 m. wide. An incandescent lamp suspended in a glass cylinder at each end of the tank provided the attracting illumination; by raising or lowering the lamp bulb in the cylinder, the light source could be located above or below the surface. Sea water entered the left-hand end of the tank and drained off at the right. A slight drift (less than 4 cm. per minute) toward the right resulted. This and other sources of left-right bias were compensated by periodically alternating the location of the light source between the right and left ends of the tank with a double throw switch. For temperatures above the seasonal sea-water temperature, the incoming water was heated. An air bubbler near the point of entrance and another near the center of the tank provided sufficient mixing so that temperature differences within the tank did not exceed 1° C. Cooling pipes, carrying a chilled ethylene glycol-water mixture, located along the walls of the tank provided uniform refrigeration when below-seasonal temperatures were required.

Variations in dissolved oxygen were achieved by recirculating the water through a tank of pure oxygen under pressure (1.5–2.0 atmospheres) or through a vacuum. These devices provided a range of 50 percent to 250 percent oxygen saturation in the experimental tank.

The intensity of the attracting lights was varied by using light bulbs of different wattages or by varying the supply voltage. The light gradient for each intensity and source position (fig. 1) was measured with a photovoltaic light meter having a waterproof housing for the sensitive element. This element was held in a plane normal to the direction of the light rays in the water. The meter was factory-calibrated for a spectral response corresponding to that of the human eye. This response is not identical to that given for herring (Blaxter, 1964), but is very similar; the difference was so small that special calibration of the instrument did not seem warranted.

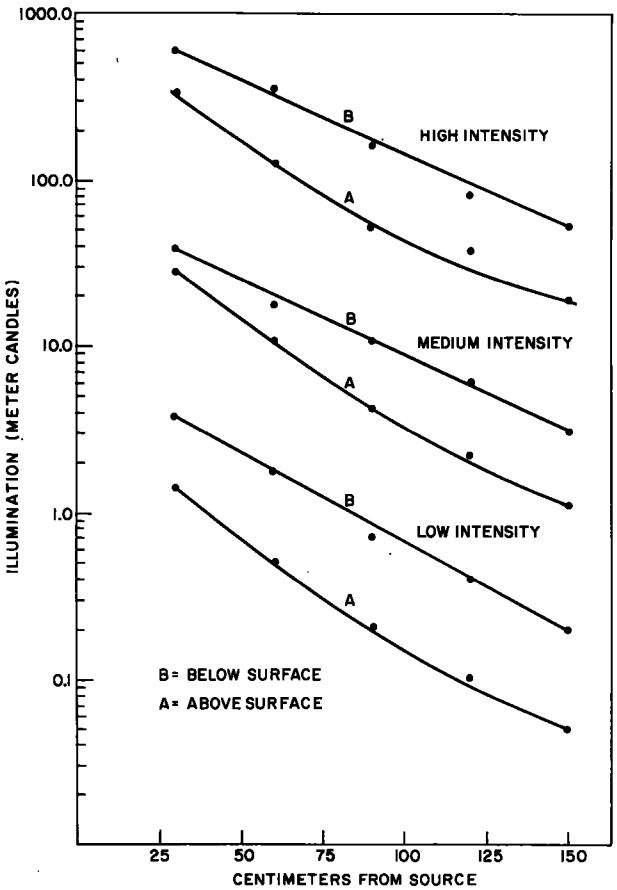

FIGURE 1.—Light gradients at the three light intensities used in the experiments.

The fish were taken at random from a storage tank and transferred to the experimental tank, where they were allowed to accommodate for periods of 30 minutes to 15 hours before each trial. Except where light or dark adaptation was at issue in the experiment, the period preceding each trial was at room illumination. I found no significant difference in the responses of individual herring allowed a half-hour or full-hour period of accommodation to the tank. Once the fish recover from the initial disturbance after transfer, it is not likely that any further time for accommodation is necessary. This factor should not affect the results of the experiments, because for any given experiment the accommodation periods of all fish were the same. Accommodation periods were progressively reduced throughout the series to save time.

No attempt was made to acclimatize the fish to arbitrarily selected temperatures because facilities for this purpose were not available. The fish were transferred from water at seasonal temperatures to the experimental tank. Because temperature acclimatization exerts a definite influence on the subsequent reactions of fish to temperature, it could conceivably affect their response to light at different temperatures. For that reason I have specified the acclimatization (=seasonal) temperature for the fish used in each experiment (table 1). It will be noticed, however, that several combinations of acclimatization and experimental temperatures produced no qualitative difference in the results of experiments where the effect of temperature was being tested.

TABLE 1.—*Summary of pretrial experience of experimental herring*

Experiment number	Accommodation period	Acclimatization temperature	Experimental temperature	
	Hours	*° C.*	*° C.*	*Month*
1	15	5	6, 12, 16	December
2	15	3	5	February
3	1-2	10-13	15-17	October
4	½-2	10-13	15-17	October
5	½-2	10	15-17	October
6	6	5	6, 12, 16	December
7	6	10-14	5-6, 15-17	July
8	3	13-16	8-10, 15-17	July-August
9	5	2-3	4-6	March
10	6	10-14	15. 5-17	June
11	6	10-14	6-9	July
12	6	13-16	15-17. 5	August-September
13	1	13	15-17	October
14	3	3	5	January
15	6	13-16	15-17. 5	August-September
16	1	14-16	15. 5-17	September

An experiment consisted of several trials in which the variables of interest were given predetermined values; each trial could be given a different set of conditions or could replicate another trial. For experimental variables that could be changed quickly (e.g. light location or intensity), several trials were completed in a single day. For conditions that required a longer time to establish (e.g. temperature or gas content), only one trial could be completed in a day, and an experiment might last several weeks. In protracted experiments of this sort, when only two treatments were involved, the trials were alternated; when several were involved in the same experiment, the trials were ordered randomly.

Two routine procedures were used. When fish were tested singly (experiments 1 to 4), the attracting light was turned on at the right end of the tank for 5 minutes, and the amount of time spent by the fish in the illuminated half of the

tank recorded. Then the illumination was switched to the left end of the tank and the time spent in that half by the fish was recorded. The illuminated half of the tank was reversed end for end every 5 minutes over 30-minute periods. The score by which the attraction to light was measured was the cumulative amount of time spent by the fish in the illuminated half of the tank.

The second routine procedure was used whenever a group of fish were tested (experiments 5 to 16). Ten randomly selected herring were placed in the tank, the attracting light on the right was turned on, and the number of fish present in the illuminated half was counted each minute for 5 minutes. The illumination was then switched to the left side, and the fish present in the illuminated half of the tank were again counted each minute for 5 minutes. The lights were, thus, alternated from end to end at 5-minute intervals until 30 counts had been made. The sum of the 30 counts was the score for groups of fish. A variant of this procedure was used in two experiments (13 and 16). Each trial lasted only 1 minute, and counts were made at 15, 30, 45, and 60 seconds. The light position remained the same throughout the period of one trial, but equal numbers of trials were made with the left side illuminated and with the right side illuminated.

In no experiment were the same fish used in successive trials; after being used once, every fish was returned to a separate holding tank and was not used again for at least 2 weeks.

Comparisons of scores between only two conditions were analyzed statistically with a "t"-test; comparisons among several kinds and levels of treatment were analyzed with a fixed-model analysis of variance.

GENERAL BEHAVIOR

After the fish had become accustomed to the experimental tank their behavior stabilized into one of three general patterns: (1) swimming regularly back and forth from one end of the tank to the other (in a loose school, if in a group), (2) remaining at one end of the tank, or (3) milling about randomly throughout the tank. After the room was darkened and the attracting light was turned on, whatever behavior pattern had been adopted by that particular fish or group of fish continued; this behavior tended to obscure the response of the herring to the attracting light. Although a brief flurry of activity near the lamp frequently occurred at the begining of each trial, the degree of attraction was not obvious by casual observation; it could be demonstrated only by repeated counts over an extended period. The fish showed no tendency to gather in any locality of optimum light intensity.

The exact behavioral mechanisms involved in the attraction of fish to artificial lights are not known, although several theories have been proposed, ranging from a straightforward positive phototaxis to a conditioned response where light is associated with food. One of the more interesting theories is that of Verheijen (1959 and in press). He suggested that an artificial light creates an unnatural light field which leads to a disoriented behavior of the fish, because "such simplified visual environments" may not "deliver adequate information to all integration levels involved in the performance of the fish's natural behavior." The net effect is one of trapping fish rather than merely attracting them.

Close observation of herring in some of my own experiments yielded clues about their behavior in an unnatural light field which may amplify somewhat the ideas of Verheijen. The typical behavior of a single herring consisted of the following events:

(1) Starting from the dark half of the tank, the fish swims slowly at first, then with increasing speed directly toward the light.
(2) Upon reaching the light, sometimes striking it squarely with its snout, the fish turns more or less broadside to it and proceeds to circle it, or swim to and fro in short courses which lie generally along the circumference of a circle around it.
(3) This behavior is frequently interrupted by movements which give the impression of confusion or disorientation. Close observation indicates that these movements are, in fact, attempts by the fish to orient its dorsal surface toward the light source. When the light is under water, these attempts lead the fish to assume momentarily vertical postures or horizontal postures on its side with its back toward the light.

(4) In retreating from the light, the fish swims in a zigzag course, the legs of which become progressively more nearly perpendicular to the direction of the light, and the fish eventually returns to it; or the legs become progressively more oblique and the fish escapes into the darkened zone.

(5) After a short stay in the dark zone, the fish repeats the entire procedure.

Many of these actions appear to be manifestations of the "dorsal light reaction" (Frankel and Gunn, 1961) in which a fish orients itself in a position so that its dorsal surface is more or less perpendicular to the direction of the light rays. Woodhead and Woodhead (1955) have described such a phenomenon in herring larvae. Under natural lighting, where the predominant direction of the light is downward, the herring can orient to the rays in its normal swimming posture, descending when the light is too strong, and rising when it decreases. When a single light source is close to the surface or beneath it, phototaxis can take place with no departure from the normal swimming posture, but dorsal orientation to the light (except when the fish is directly beneath it) requires postures that interfere with normal swimming—hence, the apparent disorientation and difficulty in escaping the influence of the light.

VARIATION IN SUSCEPTIBILITY TO LIGHT ATTRACTION

Whatever may be the effect of external conditions in modifying the response of herring to light, individual differences among the fish lead to wide variation in this response even under identical external conditions. This variability is illustrated by five experiments.

FREQUENCY DISTRIBUTION OF THE RESPONSE TO LIGHT OF INDIVIDUAL FISH

Individual fish vary in behavior as well as physical characteristics. If this variation were reasonably close to a normal distribution, the statistical treatment used in this study would be more likely to be valid than if the variation was not normally distributed. The following experiment was made to examine the variation among individual fish.

Experiment 1. Ninety herring, selected at random, were observed individually to determine the degree to which they were attracted to an underwater light of medium intensity; 30 were observed at 6° C., 30 at 12° C., and 30 at 16° C. Scoring was based on the amount of time spent in the illuminated half of the tank. The mean scores of 16.2, 17.2, and 17.8 at 6°, 12°, and 16° C., respectively, were not significantly different ($F=0.92$, $P>0.1$). The three frequency distributions each showed a reasonable tendency toward normality (fig. 2). When all the scores were combined, this tendency was more pronounced (fig. 2, dashed line).

CHANGES IN SUSCEPTIBILITY TO LIGHT ATTRACTION

If herring differ from individual to individual in their susceptibility to light attraction, do individuals vary in themselves over a period of time?

Experiment 2. To answer this question, 25 herring were fin clipped to identify individuals and tested and scored as in the preceding experiment.

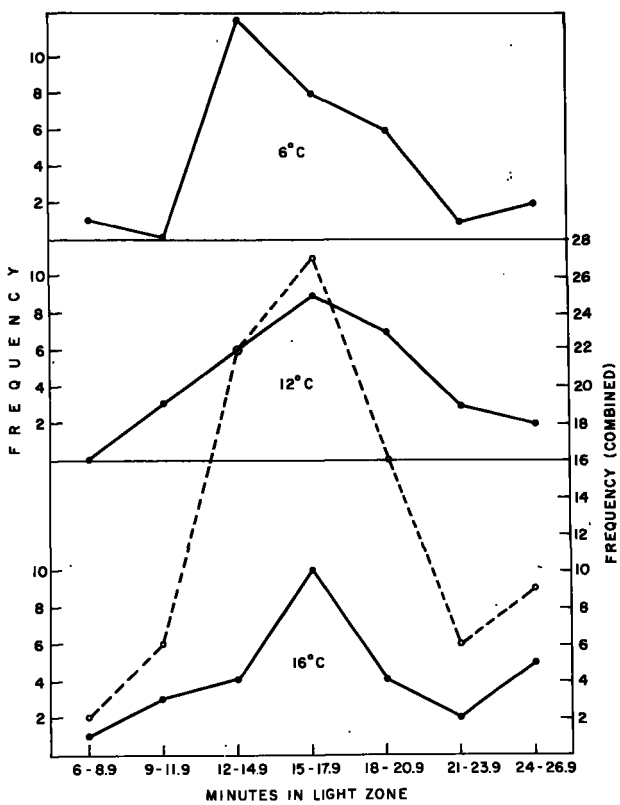

FIGURE 2.—Frequency distribution of scores (experiment 1) based on the time in minutes out of a possible 30 minutes spent by individual herring in the illuminated half of a tank. Solid lines, distribution of scores at each of three temperatures; dashed line, distribution of all scores, regardless of temperature.

They were then transferred to another tank and left undisturbed for 1 week. After this interval they were again scored as before. (Two of these fish died in the interval, so that data from only 23 were complete.)

If the degree of response is a fixed characteristic, the response should be the same on the second occasion as on the first, or if a change has occurred, it should affect all the fish more or less similarly, so that a high degree of correlation should be found between the scores in the first test and the scores in the second. Actually, some fish increased their scores and some decreased them (table 2); some changed from a positive response (more than half the time spent in the lighted zone) to a negative one. The correlation coefficient of $R=0.55$ was very weak, although it was barely significant. This result can be interpreted to mean that although individuals tend to maintain a certain inherent response characteristic, this characteristic may vary substantially with time.

TABLE 2.—*Scores (number of minutes spent in illuminated half of tank), for individual herring in two 30-minute tests, 1 week apart (experiment 2)*

First score (by rank)	Score 1 week later
Minutes	*Minutes*
25.27	16.18
24.17	19.05
23.18	16.45
21.90	19.32
21.02	19.35
20.57	20.58
20.03	14.15
19.03	18.08
18.98	10.70
18.62	15.43
18.13	14.53
18.08	14.80
17.77	19.37
17.73	18.05
15.83	16.78
15.50	17.98
14.82	20.85
14.17	8.45
14.08	13.88
13.05	9.97
12.48	7.35
12.12	13.20
12.08	11.03

EFFECT OF CONDITION ON SUSCEPTIBILITY TO LIGHT ATTRACTION

There may be many possible reasons for the variability in response among individual fish. Three reasons which readily suggest themselves are differences in sex, physical condition, and age. I did not attempt to determine the effect of sex experimentally because of the need for economy in use of specimens; determination of sex requires killing the fish. Evidence that strong sex differences occur, however, does not show in the frequency distribution of responses. If males and females differed greatly in response, one would expect some indication of bimodality to the distribution.

Experiment 3. To determine the effect of condition, 32 herring were tested individually at 15 to 17° C., and the time spent in the illuminated zone was recorded for each 30-minute trial. The medium-brilliance, subsurface illumination was reversed end for end every 5 minutes according to the routine procedure. Half of the herring were in excellent physical condition and half were starved and emaciated. The mean scores of 18.1 for the fish in good condition and 18.9 for those in poor condition were not significantly different ($F=0.22$).

EFFECT OF AGE ON SUSCEPTIBILITY TO LIGHT ATTRACTION

Two experiments were done to determine whether any differences in attraction to light could be attributed to the age of the herring; the first of these dealt with individual fish, the second with groups of fish.

Experiment 4. Nineteen herring in age group O and an equal number in age group I were tested individually according to the same procedure used in experiment 3. The mean scores of 20.4 for the O-group fish and 19.5 for the I-group fish were not significantly different ($t = 0.59$).

Experiment 5. Herring of age group O and age group I were tested in groups of 10 individuals according to the second routine procedure described under "Methods." The scores were based on the number of fish counted each minute for 30 minutes in the illuminated half of the tank, which was reversed end for end every 5 minutes. The mean scores for 10 trials with each age group were 120 for the O-group and 132 for the I-group fish; the difference was not significant ($F<1.0$).

EFFECTS OF EXTERNAL VARIABLES ON THE ATTRACTION OF HERRING TO LIGHT

EFFECT OF TEMPERATURE

The experiments in the preceding section dealt primarily with variables inherent in the fish themselves. In this and following sections the experiments deal chiefly with external variables. Evidence from experiment 1 indicated that temperature had little effect on the attraction to light of individual fish. The experiments in the present

section involve groups of fish and, as will be seen, temperature does exert a definite effect on herring in groups.

Experiment 6 (cf. experiment 1). Ninety herring, selected at random, were tested in groups of 10 individuals at three temperatures: 6°, 12°, and 16° C. Three trials were made at each temperature. The scores of 205, 129, and 121 at the three temperatures, respectively, were significantly different ($F=6.19$, $P<0.05$).

Experiment 7. The purpose and methods of this experiment were similar to those in experiment 6, except that only two temperature levels were provided and these on alternate days. In the previous experiment, trials at low temperature were made first, followed by trials at the two higher temperatures.

Five trials were made at temperatures of 5 to 6° C. and five at 15 to 17° C. The fish were taken from storage at 10 to 14° C. and held 6 hours at the experimental temperature before each trial. The mean scores were 201 at low temperature and 129 at high temperature (table 3). If the scores are treated simply as two sets of five observations, the difference in means is of marginal significance ($t=2.04$, $P=0.075$); if the scores are treated as five sets of paired observations, however, $t=10.1$ and the differences are highly significant. Because the low-temperature score for each trial was consistently higher than the immediately following high-temperature score, the analysis as paired observations seems reasonable, and the hypothesis that lower temperature increases the attraction to light is confirmed.

TABLE 3.—*Comparison of scores*[1] *for light attraction of herring at low and high temperatures (experiment 7)*

	Temp.	Score	Temp.	Score
	° C.		° C.	
	5.2	180	15.4	120
	5.7	234	16.5	155
	5.5	198	15.2	139
	5.5	179	16.2	115
	5.7	214	16.2	119
Means	5.5	201	15.9	129

[1] Score=sum of numbers of herring counted in the illuminated half of the tank at 30 1-minute intervals. Ten herring were used in each test; maximum possible score=300.

EFFECTS OF TEMPERATURE, LIGHT INTENSITY, AND LIGHT POSITION

Experiment 8. The responses of groups of 10 herring were observed at two temperature levels (8–10° and 15–17° C.), at three levels of light intensity (fig. 1), and with the attracting light either above or below the surface. Each combination of conditions was replicated once. The fish were taken from storage at 13 to 16° C. and held 3 hours at the experimental temperature before each trial. Table 4 shows the scores. The differences in response were highly significant between high and low temperature ($F=69.2$) and between above- and below-surface lights ($F=48.7$). There was also a significant interaction between light position and intensity, such that the bright light above the surface had the poorest attraction and the bright and medium lights below the surface had the greatest. The difference in response due to position of the light was significantly greater at low temperature. In general, below-surface lights were more effective at low temperature than at high.

ATTENUATION OF LIGHT ATTRACTION WITH TIME

Experiment 9. The degree to which light will hold the herring in its vicinity is a significant component of the total attraction to light. This experiment was intended to determine whether this holding effect would decrease with time, and, if so, whether such decrease was affected by light intensity or position.

TABLE 4.—*Comparison of scores*[1] *for light attraction of herring in relation to light location, light intensity, and temperature (experiment 8)*

Light intensity	High temperature (15–17° C.)		Low temperature (8–10° C.)		Mean score
	Light above surface	Light below surface	Light above surface	Light below surface	
High	135	254	122	166	146
	100	254	159	139	
Medium	192	230	159	179	167
	163	229	150	180	
Low	186	212	149	172	159
	180	217	151	164	
Mean score	159	232	148	167	

[1] Score=sum of numbers of herring counted in the illuminated half of the tank at 30 1-minute intervals. Ten herring were used in each test; maximum possible score=300.

The experiment comprised 24 trials. Each trial consisted of three phases: the first, a 30-minute series of counts on a group of 10 fish, the same as the routine procedure used in other experiments; the second, an 18-hour interval with the attracting light left on; and the third, another 30-minute series of counts like the first. The 24 trials repre-

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sented three levels of light intensity (high, medium, and low) and two light positions (above and below the surface). Each combination of lighting characteristics was replicated four times—two with the light on the left during the 18-hour interim and two with the light on the right. Table 5 gives the scores of the trials, before and after the 18-hour interim. The number of fish in the lighted zone was reduced significantly after 18 hours ($F=13.4$, $P<0.01$). This reduction was significantly greater when the lights were above the surface ($F=11.83$, $P<0.01$) than when the lights were below, but the differences in reduction associated with light intensity were not significant.

TABLE 5.—*Comparison of scores*[1] *for light attraction before and after an 18-hour interval of constant stimulus, in relation to light location and intensity (experiment 9)*

Light intensity	Before interval			After interval		
	Light above surface	Light below surface	Mean	Light above surface	Light below surface	Mean
High	109	138	134	94	130	109
	144	132		80	125	
	109	133		57	114	
	158	149		126	147	
Medium	127	209	154	80	230	133
	177	138		101	149	
	119	188		76	186	
	103	172		87	157	
Low	143	136	151	97	90	117
	224	139		136	90	
	163	133		136	143	
	147	127		138	114	
Mean	143	149		101	139	

[1] Score = sum of numbers of herring counted in the illuminated half of the tank at 30 1-minute intervals. Ten herring were used in each test; maximum possible score = 300.

EFFECT OF OXYGEN CONCENTRATION

The possible importance of oxygen concentration to the light response was suggested partly by observations that the habitat of juvenile herring was frequently supersaturated with oxygen in summer (Colton, Marak, Nickerson, and Stoddard, 1968; Stickney, 1968) and partly by a comment of Kalle (1965) that the vertical migration of herring (usually considered a response to light) might be due to depletion of oxygen in dense schools near the bottom.

Experiment 10. Groups of 10 herring were tested on alternate days in water normally saturated or highly supersaturated with oxygen before each trial. The temperature of the experiment was 15.5 to 17° C.; the mean oxygen levels were 8.1 p.p.m. (98 percent saturation) and 17.2 p.p.m. (212 percent saturation). The herring were taken from storage at 11 to 14° C., 110 to 125 percent O_2 saturation. Each trial consisted of the routine exposure to an attracting light; scores were based on the number of fish counted each minute for 30 minutes in the lighted end of the tank. The mean score for six trials in normal water was 122; that for six trials in supersaturated water was 164. The difference had a "t" value of 2.04 ($P<0.1$); treated as paired data, the differences between each pair of trial scores had a "t" value of 4.28 ($P<0.01$). The experiment seemed to indicate that supersaturation had a significant effect on the attraction of the herring to light. Subsequent experiments (11 to 13) did not corroborate these results, however.

Experiment 11. Herring were taken from holding tanks at 10 to 14° C. and 105 to 130 percent saturation of oxygen and held 6 hours under the experimental conditions before each trial. Normally saturated and supersaturated water averaging 9.6 p.p.m. (93 percent saturation) and 19.7 p.p.m. (185 percent saturation) of oxygen, respectively, at 6 to 9° C. were provided on alternate days. In five trials at each oxygen level, mean scores were 198 in the normal water, 205 in the supersaturated water. The difference is not significant ($t=0.43$).

Experiment 12. This experiment was actually a part of experiment 15 and included the additional variable of light-dark adaptation. The three levels of oxygen concentration were low (mean=5.3 p.p.m., 63 percent saturation), saturated (mean =7.9 p.p.m., 93 percent saturation), and supersaturated (mean=21.8 p.p.m., 240 percent saturation). Herring which had been adapted 6 hours to light or darkness before each trial were tested at each level of oxygen, making six combinations of experimental variables, each combination replicated five times. The herring were taken from storage at 12 to 17° C. and 100 to 124 percent saturation of oxygen and exposed 6 hours to the experimental conditions before each trial. The mean scores for ten trials at each level of oxygen were 125, 138, and 123. The difference among them was not significant ($F=0.7$).

Experiment 13. The effects of light or dark adaptation were most pronounced during the first minute of exposure to the attracting light. Because this critical time period may not have been ade-

quately monitored in the other experiments with oxygen concentration, observations were made on groups of 10 fish 15, 30, 45, and 60 seconds after the attracting light was turned on. The location of the light was alternated between right and left with each trial. Four trials were made each day; normally saturated and supersaturated water were used on alternate days. The sequence was repeated twice, making eight trials at each oxygen level, all at a mean temperature of 15.5 to 17.0° C., and mean oxygen concentrations of 7.3 p.p.m., 88 percent saturation and 16.8 p.p.m., 200 percent saturation. The mean scores of 31 and 29 were not significantly different.

The weight of evidence indicates that neither oxygen concentration nor percentage saturation has any effect on the attraction of herring to light.

EFFECT OF PREVIOUS ADAPTATION

Experiment 14. Preliminary observations showed a tendency for herring to be less strongly attracted to light if they had been kept in darkness beforehand. Therefore, for most of the experiments the herring had been held in full room illumination so that their response would be as strong as possible. Nevertheless, some specific tests seemed desirable to confirm the preliminary observations.

Sixteen trials, two each day, were made with groups of 10 herring at a temperature of 5° C. Each group was exposed to a medium-intensity, underwater light after a 3-hour period of adaptation to light or darkness just before each trial. These adaptation periods were alternated with respect to time of day, forenoon or afternoon.

Because the fish had necessarily to be held at all times other than the 3-hour adaptation period at some lighting condition or another, the possibility existed that whatever this lighting was would also influence the subsequent behavior of the fish. Therefore, half of the trials were preceded with exposure to total darkness the night before and half with full illumination. The 16 trials were arranged as follows: eight in the morning and eight in the afternoon; four of each of these eight were preceded with a 3-hour period of darkness, and four with a 3-hour period of light; two of each of these four followed an overnight period of darkness and two an overnight period of light. An analysis of variance showed significant variation only with respect to the 3-hour pretrial light- or dark-adaptation period ($F=5.8$, $P=0.05$). The effects of overnight lighting and time of day were of doubtful significance ($F=3.4$, $P=0.1$, and $F=2.6$, $P>0.1$, respectively). The scores are shown in table 6. Pretrial adaptation to darkness reduced the effectiveness of light attraction.

TABLE 6.—*Comparison of scores* [1] *for light attraction of herring in relation to prior light experience and time of day (experiment 14)*

Time of day	Overnight darkness		Overnight light	
	Dark [2]	Light [2]	Dark [2]	Light [2]
AM	103	90	127	205
	105	153	132	134
PM	100	168	146	193
	155	162	136	170
Mean score	114	143	128	175

[1] Score=sum of numbers of herring counted in the illuminated half of the tank at 30 1-minute intervals. Ten herring were used in each test; maximum possible score=300.

[2] Light condition for 3 hours preceding trials.

Experiment 15. This experiment was done later in the year than experiment 14 at the higher temperature range of 15 to 17.5° C. No allowance was made for any previous light experience of the fish prior to a 6-hour light or dark period of adaptation before each trial. The experiment also included the additional variable of oxygen concentration and was actually a part of experiment 12. The mean score for 15 trials preceded by a 6-hour dark period was 122; that for 15 trials preceded by a 6-hour light period was 136. The difference between them was not significant ($F=1.48$, $P>0.2$). Apparently, previous adaptation to light or dark makes little difference in the response of herring to light at high temperature.

Experiment 16. The pretrial adaptation of herring to light produced the strongest positive response when the trials were made at low temperature. The most marked attraction in experiment 14 occurred during the first minute of the trial: the scores during the first minute differed by 57 percent; the total scores differed by only 25 percent. This fact suggests that light or dark adaptation affects the initial attraction to light more than it affects the tendency for the light to hold the fish.

Although the total scores at high temperature in experiment 15 did not differ significantly between light- and dark-adapted herring, the first minute scores were somewhat (though not significantly) higher for light-adapted herring. Experiment 16

demonstrated that the first minute scores for light-adapted herring were, in fact, significantly higher even at high temperature than those for dark-adapted herring. Four trials at 15 to 17.5° C. were made each day for 4 days; each trial was preceded by a 1-hour period of light or darkness. Counts of the fish were made at 15, 30, 45, and 60 seconds after the attracting light was turned on. The end of the tank illuminated, left or right, was alternated with each trial. The mean score for the fish adapted to light for 1 hour was significantly higher ($F=32.7$, $P<0.01$) than the mean score for the dark-adapted fish (table 7). A significant bias for one side of the tank also was apparent in this experiment. Such a bias sometimes occurred for unknown reasons and made left-right alternation of the illuminated side of the tank a necessary part of the procedure in all experiments.

This experiment showed that previous adaptation to light increases the initial attraction of the herring to light regardless of temperature; on the other hand, the holding effect of the light was weakened at high temperature regardless of the prior adaptation.

TABLE 7.—*Comparison of scores*[1] *for light attraction of herring during first minute of exposure, in relation to prior light experience (experiment 16)*

Location of light	Herring	
	Light adapted	Dark adapted
Left	31	36
	37	33
	29	25
	34	21
Right	23	5
	30	5
	30	10
	33	7
Mean score	31	18

[1] Score = sum of numbers of herring counted in the illuminated half of the tank at four 15-second intervals. Ten herring were used in each test; maximum possible score = 40.

ANALYSIS OF BEHAVIOR IN RESPONSE TO LIGHT

The attraction of herring to artificial lights is a composite behavior pattern made up of two general categories of responses: those that draw the fish toward the light and those that hold the fish under the light's influence. The initial attraction seems to be a (usually) positive telotaxis, defined by Frankel and Gunn (1961) as direct attainment of orientation, without deviations, to a source of stimulus as if it were a goal. This response is stronger in some individuals than in others and in a few may even be negative (away from the light).

The holding power of the light, on the other hand, is determined by several, often dissimilar, responses of the fish. One of these is the dorsal light reaction discussed earlier; it holds the fish near the light by interfering with normal swimming movements which would lead to escape. Another is photokinesis, where general activity and swimming speed increase with increasing light intensity; this response works in opposition to the dorsal light reaction, tending to cause dispersal. Adaptation and fatigue probably accompany continued exposure to the light and may weaken both of the other reactions. Finally, there is the startling or shock effect of sudden changes in light intensity, which may repel the fish, as if by fright.

The response of fish to light is determined by the way in which conditions influence these behavioral components. Some of these reactions can be summarized as follows: Temperature affects primarily the degree to which the fish are held under the influence of the light, probably through its effect on their activity; higher temperature increases general activity, which in turn tends to cause dispersal. The position of the light above or below the surface also affects the holding power of the light. Herring are accustomed naturally to light rays directed downward from the surface, and light from a source below the surface is likely to produce orientation which interferes with normal swimming and escape from the lighted zone. Previous adaptation affects primarily the initial attraction to the light, which is stronger in light-adapted fish than in dark-adapted fish.

An attempt to measure the startle effect of light indicated that whenever the attraction or holding power of the light was strong, the startle effect was less pronounced than when the attracting or holding power was weak. The startle effect was measured by the ratio of the number of fish in either side of the tank before the light was turned on to the number present immediately afterwards. A correlation of -0.957 was found between these ratios and the scores for 10 experiments selected

to include those circumstances favorable to light attraction and those unfavorable.

The difference in response to light shown by individual fish and by fish in groups under otherwise similar conditions may be another significant aspect of behavior. The data from experiment 1, in which the responses of 90 individual herring to light were tested at three different temperatures, and from experiment 6, in which the responses of 90 herring were tested in groups of 10 at the same three temperatures are an example. If the fish tested individually are combined arbitrarily into three groups of 10 for each temperature, and the mean score for each group is expressed as a percentage of the maximum possible score, measures of variance among the groups can be calculated. Similarly, the variance among the scores, expressed as a percentage of the maximum possible score, can be calculated for the actual groups of 10 fish observed in experiment 6. A comparison shows that the variance among the scores of the actual groups of 10 fish is significantly greater than the variance among the scores of the arbitrarily created groups of fish tested individually. In fact, the variance among the scores of the actual groups is not significantly different from the variance among the scores of individuals. These facts imply that the collective response of 10 herring in a group is not simply an average of their individual responses. Instead, the collective response seems to reflect the individual responses of only one or two fish in the group.

To explain the apparent lack of thermal influence on fish individually in contrast to the significant thermal influence on groups, I suggest the following hypothesis. Most herring are only feebly influenced by temperature in their response to light. The preponderance of fish in this category causes the average response to appear uninfluenced by temperature when each fish responds as an individual, even though a few individuals may be strongly influenced. When the fish are in groups, however, the weakly influenced majority respond not so much to the stimulus itself as to the strongly influenced minority, whose behavior dominates the group. I believe that in this interaction lies the significance of the school in fish behavior: the interaction provides to the group a sensitivity and an ability not possessed by individuals to react in an unequivocal manner to a situation.

RESPONSES OF HERRING TO LIGHT AND THEIR APPLICATION IN THE FISHERY

Without doubt attraction to artificial lights at night is a significant behavioral response of herring, and it is potentially useful in the herring fishery. The question is: Under what conditions is this response brought out most strongly and what tactics in using lights can be most effectively employed?

Most of the evidence indicates that a submerged light is more effective than one above the surface. One reason is that the entire output of the underwater light is used, whereas a large portion of the light from above the water is reflected from the surface. The submerged light is also more uniform: the rays do not flicker from the effect of a ruffled surface. Moreover, the submerged light has an improved attracting effect which is independent of its greater efficiency. A submerged light which produced only 1/10 to 1/1,000 the underwater illumination of a light above an unruffled surface proved to be the more effective in laboratory experiments. Because of refraction, the rays from a light above the surface project sharply downward, even at some distance from the light source. It may be that the direction of the rays in relation to the position of the fish are important, and that rays from above the surface approaching the vertical tend to repel herring. The light from the sun, sky, or a bright moon would be of this nature; all of these light sources tend to keep the herring from the surface and may be the cause of the characteristic diurnal vertical migrations of herring.

Evidence from my experiments and also from other studies shows that the brightest lights are not necessarily the most effective for attracting herring. Although a brighter light will have a greater range and can be seen by fish at a greater distance, the illumination within a certain radius may exceed the optimum and tend to repel the fish even if they are attracted up to that radius. To obtain maximum range while still attracting nearby fish, certain manipulations of the light have been used effectively. The simplest method is to dim the light gradually (Gauthier, in press; Kurc, in press; Ström, in press). Another scheme was described by Sasaki (1959): A series of lights of optimum brilliance extend some distance from

the fishing operation. The outermost light is turned on for a time until a substantial number of fish are attracted. This light is then extinguished, and another somewhat closer to the fishing operation is illuminated. Each light in the series is lighted and extinguished in sequence, attracting in turn the fish gathered about the preceding one.

Besides the properties of the light itself, certain factors of the environment govern the effectiveness of the light, especially in relation to the time of day or time of year it is used. Kawamoto (1959) showed that in some species of fish the light-seeking tendency was stronger in the daytime than at night. Tamura (1959), discussing this phenomenon and certain physiological changes in the eye of the fish when adapted from light to darkness, suggested "this may be one of the fundamental reasons why fishing with the use of light is usually more effective before than after midnight." The results of my own experiments with herring show a greater attraction to light of light-adapted fish, especially the initial attraction. All of these observations suggest that fishing with a light would be most effective shortly after dusk.

I can find no reference to the effect of temperature on the response of herring to light except as it relates to their passage through the thermocline; there are records, however, indicating that temperature does affect the response to light of other species of fish. Andrews (1946) showed that the positive phototaxis of suckers (*Catastomus*) was weakened at high temperature; Grubišić (1962) stated that the attraction of sardines (*Sardina pilchardus*) to light was weaker in the summertime than at other seasons and that this weakness was "more evident when the summers are more than normally hot."

Because the attraction of herring to light seems also to be weakened at high temperature, success in fishing for them with artificial lights might well depend in part on the season of the year and the temperature characteristics of particular localities. Moreover, temperature seems not only to affect directly the attraction to light, but also to modify the effects of light position and previous adaptation to light or darkness.

My purpose in the experiments involving temperature was limited to finding out whether temperature had any effect at all. Obviously, it did, but the critical values of both experimental and adaptation temperatures need yet to be defined. It is possible that the temperature preferendum described elsewhere (Stickney, in press) represents the critical point above which the light response weakens.

The use of lights in the herring fishery of the Canadian and United States Atlantic Coast has been in disfavor for some time and is even illegal in many places. Even where it is still legal, it is a method of little importance probably because fishermen believe that lights frighten the herring away (Scattergood and Tibbo, 1959). Fishing at night is carried on with as little light showing as possible. Because above-water lights, excessively bright lights, and lights suddenly flashed on or moved about do apparently frighten herring, the caution used in showing lights is probably justified. On the other hand, practical experience and biological evidence indicate that lights properly used under some circumstances can attract herring effectively. It would seem that artificial lights used in accordance with what is known about herring behavior would provide an extremely useful method for controlling the herring schools so that they would be in locations most conducive to setting purse seines or stop seines around them.

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VARIATIONS IN MARINE ZOOPLANKTON FROM A SINGLE LOCALITY IN HAWAIIAN WATERS

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ABSTRACT

Data on marine zooplankton and hydrography were obtained off Oahu, Hawaii, at monthly intervals from June 1957 through December 1958.

Samples collected at 3-hour intervals for 48 hours in June 1957 were examined for diel variation. Volumes of zooplankton exhibited the expected sinusoidal variation during the first 24 hours, but not during the second. High volumes during the second morning were attributed to the presence of an unidentified diatom that retarded drainage of moisture during determination of volumes of zooplankton. Variations in abundance were sinusoidal for Ostracoda, Euphausiacea, Pteropoda, and fish larvae. Similar variations in surface temperature and depth from the surface to the top of the thermocline were attributed to solar heating and internal waves, respectively.

The 19 monthly samples showed correlations between volumes of zooplankton and salinities and between volumes of zooplankton and depth to the top of the thermocline. The 19 months were divided into nine successive periods, each with a temperature-salinity curve differing from that of the preceding and following periods. Volumes of zooplankton and the abundance of Siphonophora, Chaetognatha, Euphausiacea, decapod Crustacea, and Pteropoda increased when portions of the temperature-salinity curves greater than 35.0‰ increased during the nine periods; and, conversely, the volumes of zooplankton and the abundance of these groups of zooplankters decreased as the amount of water with salinity greater than 35.0‰ decreased.

Once every month from June 1957 through December 1958, members of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, collected hydrographic and meteorological data from a station located at lat. 21°10.3′ N., long. 158°19.0′ W. for the Island Observatory Project of the International Geophysical Year Oceanographic Program (Scripps Institution of Oceanography, 1965). This position, referred to as the IGY station, is about 32 km. southwest of Barbers Point, Oahu, where the depth of the water is about 3,000 m.

Samples of zooplankton were also collected at the IGY station for studies of variations in the standing crop and composition of marine zooplankton in relation to environmental factors at a single locality in Hawaiian waters. The results showed that volumes of zooplankton were high in waters of high surface and subsurface salinities.

METHODS

The samples of zooplankton were collected with a net having a mouth diameter of 1 m.; a flowmeter was mounted in the center of the opening. The body of the net was constructed of synthetic fiber of 0.656 mm. aperture width; the rear section, including the cod end, was made of synthetic fiber of 0.308 mm. aperture width. Detailed descriptions of the construction of the net and the method of making the tow have been presented by King and Demond (1953).

The nets were towed obliquely from the surface to a depth of 60 m. and back in one-half hour. In June 1957, such hauls were made at 3-hour intervals over a 48-hour period to measure diel variations. In the succeeding months, four half-hour hauls were made each time the station was occupied: two successive daylight hauls starting at about 1600 l.s.t. (local standard time) and two successive night hauls between 2100 and 0300 l.s.t.

The methods of processing and determining the volumes of the samples of zooplankton have been described by King and Hida (1954, 1957a). Counts of various groups of plankters were made on the night samples.

For the counts, an aliquot of a sample was first placed in a counting cell (a 15 by 20 by 1.5-cm.

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plastic dish) which had 300 subdivisions ruled into its bottom. The organisms in 40 randomly selected squares were identified and counted under a dissecting microscope. The estimated number of a group of organisms in 1,000 m.^{3} of water was calculated by the following formula (modified from King and Demond, 1953):

$$E=\frac{CA}{fanW}1{,}000$$

where E=number of organisms per 1,000 m.^{3} of water
C=counted number of organisms
A=area of counting cell (300 cm.^{2})
f=fraction of total sample in the counting cell
a=area of square (1 cm.^{2})
n=number of squares counted (40)
W=cubic meters of water strained by net

Usually, on each visit to the IGY station, two hydrographic casts were made, one during the highest tide and the other during the lowest tide. Ordinarily, each cast was from 0 to 500 m. depth and consisted of 12 Nansen bottles, but on some occasions the casts were deeper. Temperature and salinity data were obtained with each cast, and with a few exceptions, oxygen and inorganic phosphate were also measured. Additional temperature data were obtained with bucket thermometers and bathythermographs.

Salinity determinations were made by a modification of the Knudsen method (Van Landingham, 1957); inorganic phosphate determinations were made with a Beckman [1] spectrophotometer.

Temperature, salinity, phosphate, and oxygen values used in the study were averaged as follows:

Surface value: average of measurements obtained at water surface during high tide and low tide.

0 to 60 m. value: average of measurements at depths of 0, 10, 20, 30, 40, 50, and 60 m. during high tide and low tide.

200 to 300 m. value: average of values at 15-unit increments between the 400 and 300 thermosteric anomaly surfaces on a temperature-salinity plot. These two anomaly surfaces represented approximately 200 and 300 m., respectively.

[1] Trade names referred to in this publication do not imply endorsement of commercial products.

Vertical temperature distribution: isotherms were contoured on the basis of the average temperatures at the following depths: 0, 9.2, 15.2, 30.5, 45.8, 61.0, 76.2, 91.5, 100.6, 122.0, 149.4, 152.5, 183.0, 199.8, 213.5, 244.0, and 274.5 m. Readings were limited to a maximum of five bathythermograms per month.

DIEL VARIATIONS

In central Pacific waters, diel variation in volumes of zooplankton and in abundance of certain zooplankton has been shown to vary as the curve of the sine function (King and Hida, 1954; Legand, 1958; Nakamura, 1967); the peak equated to midnight. The volumes and abundance of zooplankters determined from samples obtained at 3-hour intervals from June 21 to 23, 1957, were examined for similar variations. Temperatures and depths to the top of the thermocline for this period were also examined for diel variations.

VOLUMES OF ZOOPLANKTON

The volumes of zooplankton obtained for the 48-hour series ranged from a low of 13 cc./1,000 m.^{3} of water strained to a high of 40 cc./1,000 m.^{3}, with a mean of 26 cc./1,000 m.^{3} (fig. 1). The volumes of the samples obtained during the night were greater than those of the samples collected by daylight; the night to day ratio was 1.3 : 1. The greater abundance of zooplankton in darkness has been attributed by investigators to some combination of an upward migration by the zooplankters and an increased avoidance of the net by some organisms in daylight (King and Hida, 1954, 1957a; Fleminger and Clutter, 1965; Brinton, 1967).

The volumes from the 48-hour series appeared to conform approximately to a sinusoid for the first 24-hour period but not for the second. The volumes remained high through the second morning. An unusually large amount of an undetermined species of diatom was present in samples 11, 12, 15, and 16. The greater resistance of these samples to moisture drainage than of those without diatoms resulted in a greater determination of wet volume. This fact may have explained the unusually high volumes in samples 12, 15, and 16. On the other hand, the volume of sample 11 did not appear to be unusual even though it too contained diatoms.

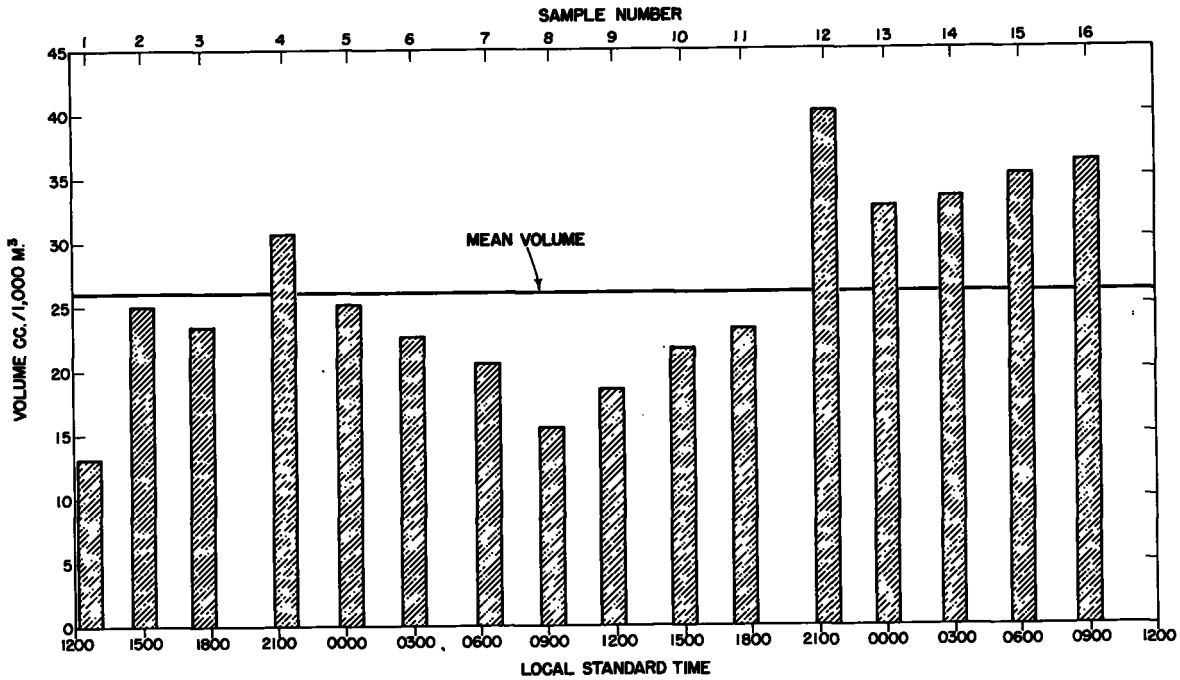

FIGURE 1.—Variations in volumes of zooplankton over a 48-hour period, June 21–23, 1957, at the IGY station. Sunrise during this period was at 0503 and sunset at 1846 hours.

COMPOSITION OF ZOOPLANKTON

Abundance of groups of plankters expressed as average numbers per 1,000 m.³ of water strained and as average percentages of total numbers of plankters is summarized in table 1. By far the most numerous organisms in the samples were copepods, which on the average constituted about 60 percent of all organisms present. Chaetognatha and *Halosphaera viridis*,[2] almost equal in average abundance, were the second and third most common organisms in the samples. Numerically, each averaged less than 10 percent of the copepods.

Distinct diel variations, with greater numbers during darkness, were exhibited by Ostracoda, Euphausiacea, Pteropoda, and fish larvae (fig. 2). Amphipoda exhibited such a diel variation only during the second half of the series (fig. 2). In addition to the aforementioned groups, Annelida (Polychaeta) and calanoid Copepoda have been shown previously to exhibit distinct diel variations in Hawaiian waters (Nakamura, 1967). In this study, these two groups did not show the characteristic peaks of abundance during darkness. Perhaps if specific or generic identifications had been made diel fluctuations would have been revealed, for Nakamura (1967) found that the following genera of calanoid copepods were concentrated in the upper waters during darkness: *Pleuromamma*, *Neocalanus*, *Candacia*, *Undinula*, and *Euchaeta*. In the present study abundance of Heteropoda reached a peak during daylight as well as at night.

TABLE 1.—*Average abundance and average percentage composition of various plankters for 16 samples of the 48-hour series*

Plankters	Average abundance	Average composition
	No./1,000 m.³	*Percent*
Halosphaera[1]	1,654	5.6
Foraminifera	775	2.6
Radiolaria	572	1.9
Siphonophora	1,088	3.7
Chaetognatha	1,626	5.5
Annelida	132	.4
Calanoid Copepoda	17,788	59.8
Noncalanoid Copepoda	1,024	3.4
Ostracoda	866	2.9
Euphausiacea	664	2.2
Amphipoda	1,189	4.0
Decapod Crustacea	1,075	3.6
Pteropoda	290	1.0
Heteropoda	147	.5
Gastropod larvae	64	.2
Pelecypoda	50	.2
Thaliacea	51	.2
Appendicularia	422	1.4
Fish larvae	129	.4
Fish eggs	35	.2
Others	82	.3

[1] *Halosphaera viridis*, a phytoplankter, numerous in all samples.

[2] This phytoplankter was present in every sample and was included in all counts.

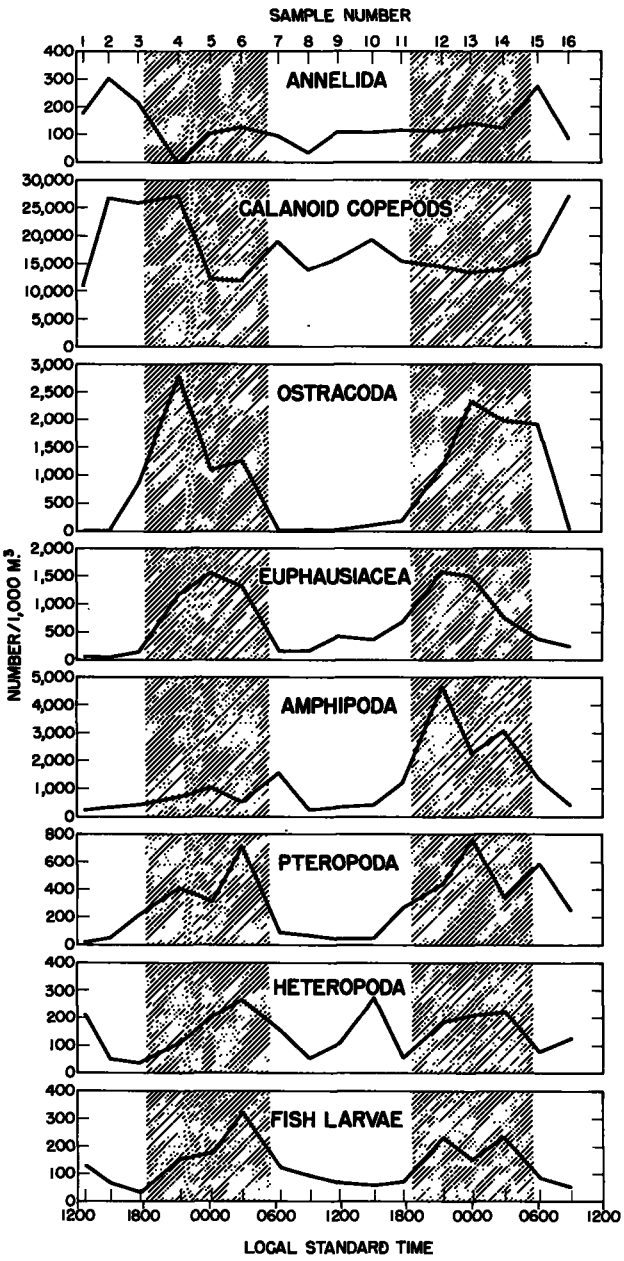

FIGURE 2.—Variation in the abundance of various groups of zooplankters during June 21–23, 1957, at the IGY station.

TEMPERATURE

The diel variation in surface temperature (fig. 3) was attributed to solar heating during the day and cooling at night. A subsurface thermal disturbance was evident between 0400 and 1200 hours, June 22. It was probably caused by advection; however, unusual changes in the volumes of zooplankton did not occur during the thermal disturbance.

DEPTH FROM SURFACE TO TOP OF THERMOCLINE

The sinusoidal variation in the depth from the surface to the top of the thermocline (fig. 3) showed fluctuations probably caused by internal waves. The variations in depth to the top of the thermocline, however, did not appear to influence the abundance or composition of the zooplankton during the 48-hour period. The depths for the hauls of zooplankton in this series ranged from 52 to 65 m. The depth from the surface to the top of the thermocline ranged from 23 to 61 m. Sample 8 was the only one collected entirely within the isothermal layer above the thermocline. The volume of sample 8 was not unusual. Chaetognatha had their least abundance and Pelecypoda their greatest abundance in this sample.

CORRELATIONS BETWEEN ZOOPLANKTON AND PHYSICAL AND CHEMICAL FACTORS

King and Hida (1954, 1957b), in their studies of the distribution and abundance of zooplankton in Hawaiian waters, were unable to show a consistent relation between the standing crop and temperature, surface phosphate, dissolved oxygen, and depth from the surface to the top of the thermocline. Analyses of their data from seven cruises gave one statistically significant correlation ($P<0.05$) between zooplankton and temperature (at 10-m. depth) and one significant correlation ($P<0.01$) between zooplankton and surface phosphate. King and Hida's samples were taken from a large area around the Hawaiian Islands.

Consistently high or low standing crops regardless of changes in the environment (McGary 1955; Seckel, 1955) have been found in certain areas in Hawaiian waters. For example, King and Hida (1954, 1957b) found consistently low volumes of zooplankton from immediately east of the island of Hawaii.

The results of the correlation analyses for the present study, where sampling was confined to one locality, are summarized in table 2. Volumes of zooplankton were examined in relation to the physical and chemical data for the surface, 0 to 60 m. (range in depth of the hauls for zooplankton),

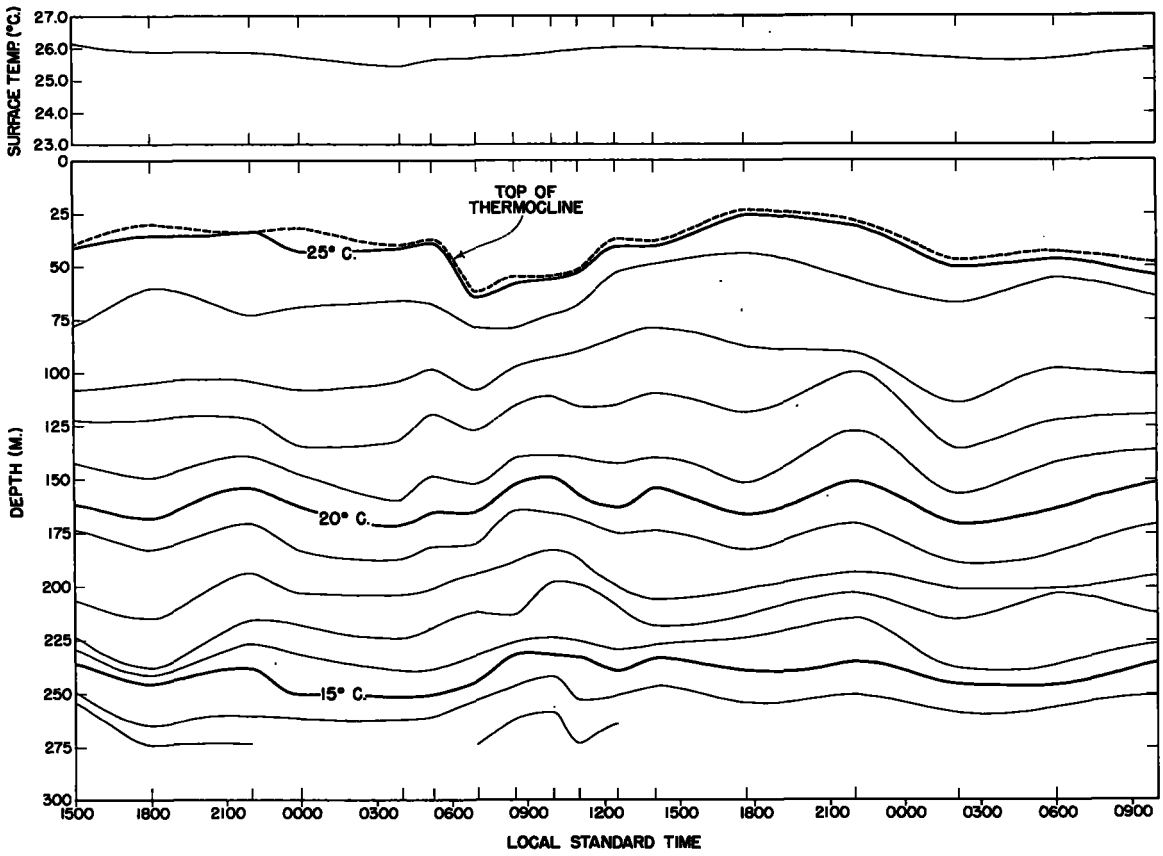

FIGURE 3.—Vertical distribution of temperature during June 21–23, 1957, at the IGY station.

TABLE 2.—*Summary of correlations between volumes of zooplankton and certain physical and chemical environmental factors*

First variate (X_1)	Second variate (X_2)		Degrees of freedom	Correlation coefficient (r)
Surface salinity (°/₀₀).	Zooplankton volume (cc./1,000 m.³).	Night hauls.	16	0.397
		Day hauls..	16	**.655
Surface oxygen (ml./l).	Zooplankton volume (cc./1,000 m.³).	Night hauls.	14	−.029
		Day hauls..	14	.228
Surface inorganic phosphate (μg.at./l).	Zooplankton volume (cc./1,000 m.³).	Night hauls.	13	−.132
		Day hauls..	13	−.227
0–60 m. salinity (°/₀₀).	Zooplankton volume (cc./1,000 m.³).	Night hauls.	16	.464
		Day hauls..	16	**.706
0–60 m. temperature (° C.).	Zooplankton volume (cc./1,000 m.³).	Night hauls.	16	.025
		Day hauls..	16	−.236
200–300 m. salinity (°/₀₀).	Zooplankton volume (cc./1,000 m.³).	Night hauls.	16	*.507
		Day hauls..	16	.455
Depth to top of thermocline (m.).	Zooplankton volume (cc./1,000 m.³).	Night hauls.	16	*−.524
		Day hauls..	16	*−.544

*Significant at 5-percent level.
**Significant at 1-percent level.

and about 200 to 300 m., and also the depth from the surface to the top of the thermocline. Changes in volumes of zooplankton and in physical and chemical factors of the environment during the 19 months are illustrated in figures 4, 5, and 6. Surface values are given in table 3.

Except for June 1957 and October 1958, the volumes of zooplankton obtained at night were greater than those collected by day (fig. 4). The ratio of night to day volumes ranged from 0.9 : 1 to 3.3 : 1 and averaged 1.8 : 1.

Volumes of zooplankton showed close correlations with salinities and depths of the isothermal layer but not with other environmental factors. Positive correlations were significant at either the 5 percent or 1 percent probabilities between volumes of zooplankton for day hauls and salinities at the surface and at 0 to 60 m., and for night hauls and salinities at 200 to 300 m. (table 2). Correlations between volumes of zooplankton for night hauls and salinities at 0 to 60 m. and for day hauls and salinities at 200 to 300 m. were very close

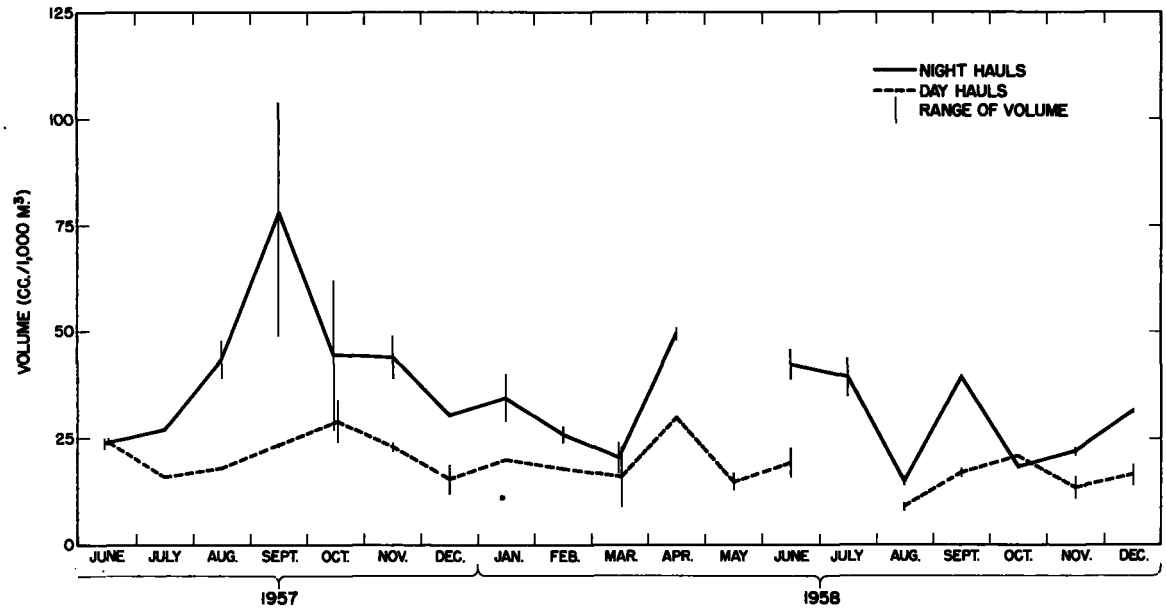

FIGURE 4.—Monthly variations in volumes of zooplankton collected by night and by day at the IGY station from June 1957 to December 1958.

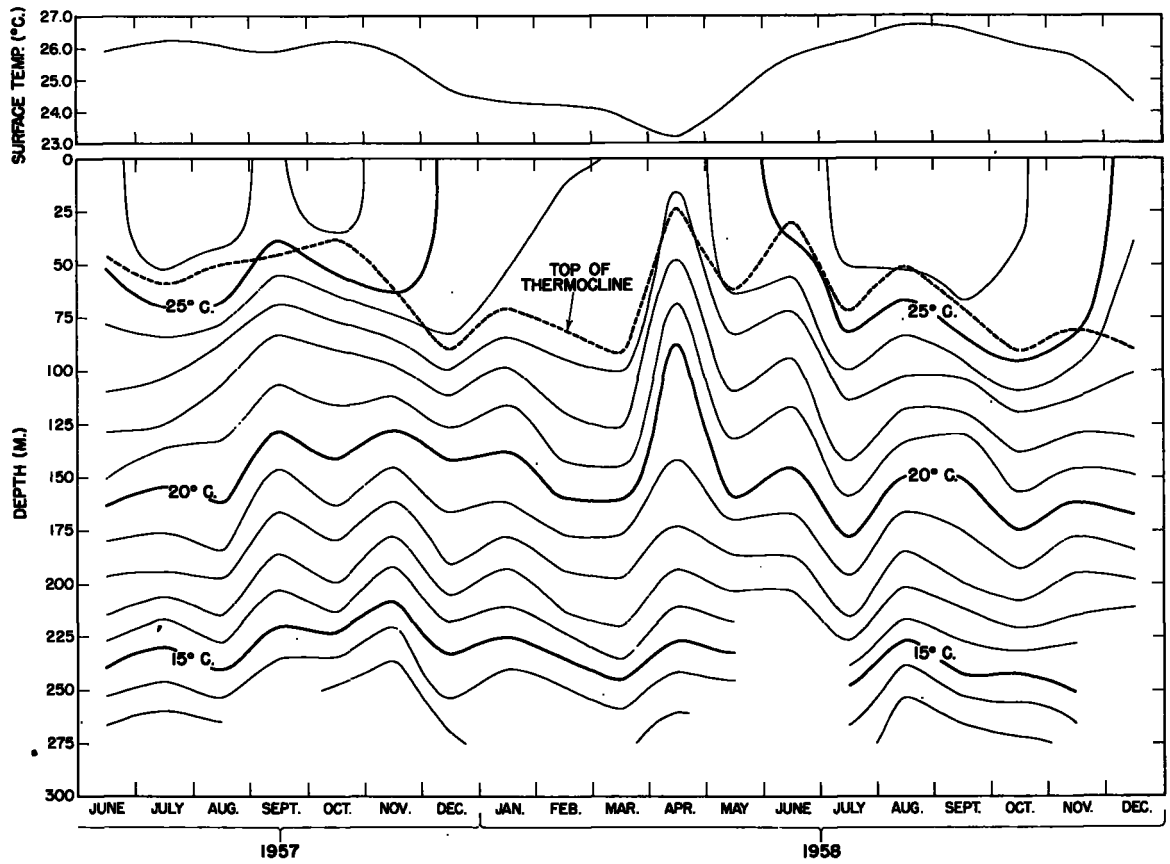

FIGURE 5.—Monthly vertical distribution of temperature at the IGY station from June 1957 to December 1958.

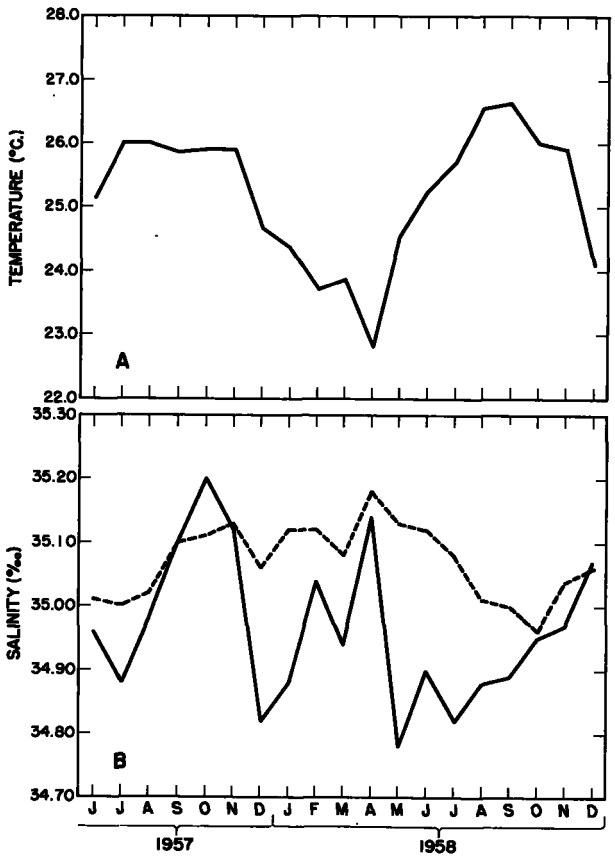

FIGURE 6.—Monthly variation in temperature and salinity at the IGY station from June 1957 to December 1958. A. Mean 0 to 60 m. temperatures. B. Mean 0 to 60 m. salinities (solid line) and mean 200 to 300 m. salinities (dashed line).

to significance at the 5 percent probability (for $P = 0.05$ and d.f. = 16, $r = 0.468$). Negative correlations were significant between volumes of zooplankton for both night and day hauls and depths from the surface to the top of the thermocline. Neither temperature, oxygen, nor inorganic phosphate was correlated with volumes of zooplankton.

We believe the significant relations between zooplankton and salinity and between zooplankton and the thickness of the isothermal layer resulted from the advection of different types of water into the Hawaiian area. The biomass of zooplankton was higher in waters of high salinity.

ZOOPLANKTON AND TEMPERATURE-SALINITY CURVES

Seckel (1962) indicated that the Hawaiian Islands are located near the northern boundary of the transition zone between two major types of surface water: (1) the high-salinity (surface values >35.0‰) North Pacific Central Water, and (2) the low-salinity (surface values <34.2‰) North Pacific Equatorial Water. These water types corresponded approximately with the subsurface water masses as defined by Sverdrup, Johnson, and Fleming (1942). Seckel (1962) classified the California Current Extension, which forms the core of the transition zone, as a third type. He showed that the boundaries of these water types shifted seasonally and affected the type of water to be found near Oahu.

TABLE 3.—*Monthly values of surface salinity, inorganic phosphate, and oxygen during low and high tides at the IGY station*

Month	Salinity °/₀₀		Phosphate μg.at./l		Oxygen ml./l	
	Low tide	High tide	Low tide	High tide	Low tide	High tide
1957						
June	34.97	34.97	0.22	0.20	4.29	4.32
July	34.87	34.88	.29	.24	4.47	4.46
August	34.96	34.96	.20	.22	4.79	4.78
September	35.07	35.12	.13	.16	.....	4.45
October	35.19	35.16	.10	.16	4.53	4.51
November	35.12	35.12	.11	.16	4.78	4.64
December	34.72	34.81	3.65	.....	4.58	4.56
1958						
January	34.81	34.85	.12	.13	4.79	4.69
February	35.03	35.05	.22	.20	4.85	4.84
March	34.94	34.96	.64	1.60	4.60	4.66
April	35.10	35.07	.....	.....	.....	.....
May	34.80	34.77	.06	.62	4.55	4.62
June	34.90	34.82	.....	.....	4.08	4.18
July	34.81	34.80	.49	.70	4.77	4.80
August	34.91	34.89	.39	.22	4.43	4.55
September	34.86	34.87	.....	.....	4.55	4.64
October	34.94	34.96	.21	.23	.....	4.40
November	34.96	34.94	.11	.10	.....	.....
December	34.94	35.05	.....	.35	.....	4.64

Our data were analyzed from the standpoint of advection of different types of water as indicated by changes in the temperature and salinity during the 19 months of observation. The data were divided into the following nine chronological periods (fig. 7) on the basis of the similarity in the temperature-salinity (T-S) curves for successive months: June to July 1957, August 1957, September to November 1957, December 1957 to March 1958, April 1958, May 1958, June to July 1958, August to November 1958, and December 1958. Each period had temperature and salinity characteristics that were different from the preceding and succeeding periods. The average monthly (0–60 m.) temperatures, the average monthly salinities (0–60 m. and 200–300 m.), and the average depth from the surface to the top of the thermocline for the nine periods are illustrated in figure 8.

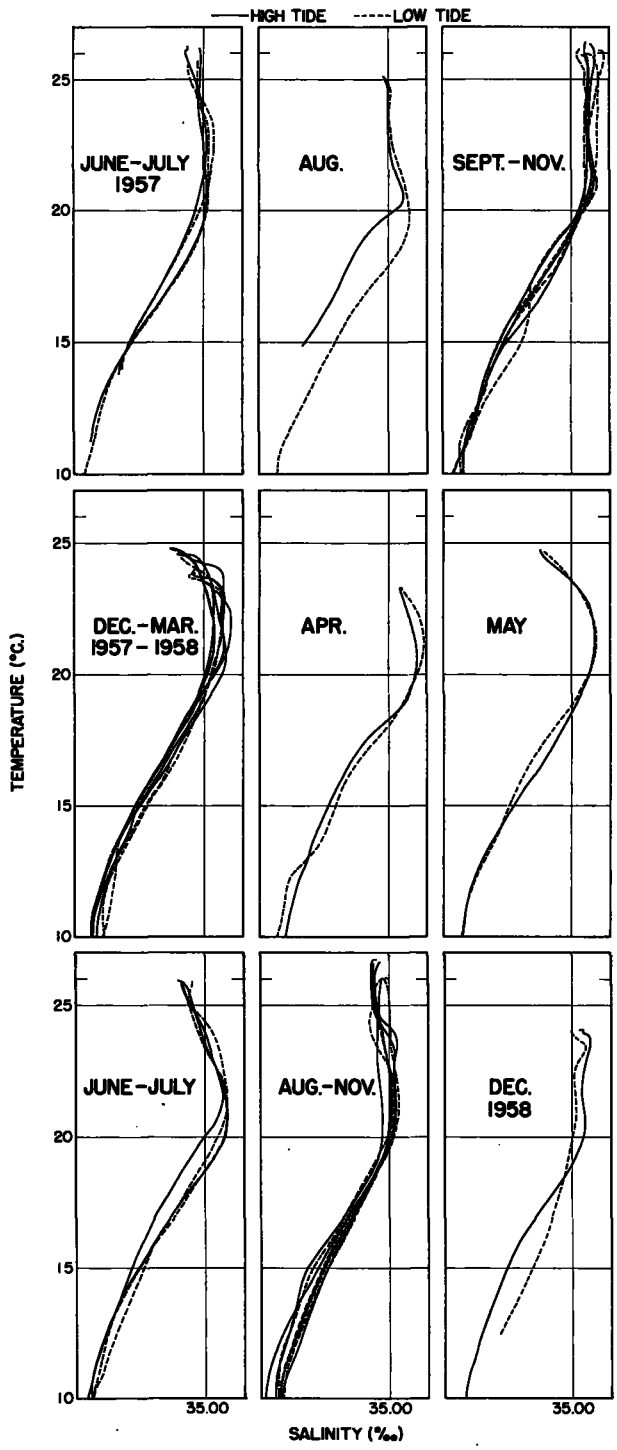

FIGURE 7.—Monthly temperature-salinity relation at highest high tide and lowest low tide at the IGY station by periods.

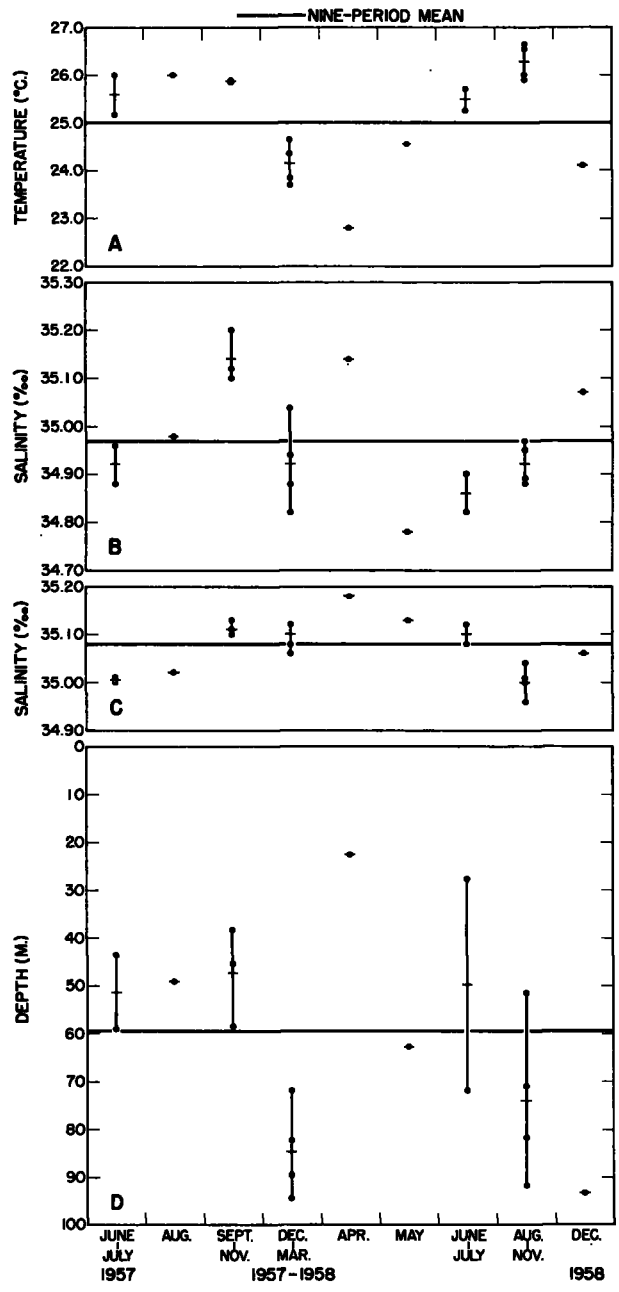

FIGURE 8.—Physical and chemical characteristics of the nine periods. A. Average 0 to 60 m. temperatures. B. Average 0 to 60 m. salinities. C. Average 200 to 300 m. salinities. D. Average depth from the surface to top of thermocline.

TABLE 4.—*Average abundance (No./1,000 m.³) of various plankters from samples taken at night at the IGY station*

Plankters	Period and (in parentheses) number of samples								
	June, July 1957 (2)	Aug. 1957 (1)	Sept., Oct., Nov. 1957 (3)	Dec. 1957, Jan., Feb., Mar. 1958 (4)	Apr. 1958 (1)	June, July 1958 (2)	Aug., Sept., Oct., Nov. 1958 (4)	Dec. 1958 (1)	Eight-period mean (8)
Halosphaera [1]	5,392	1,771	3,047	3,569	5,284	1,582	2,400	5,102	3,518
Foraminifera	660	551	283	286	1,308	94	274	559	502
Radiolaria	204	394	158	156	366	38	142	298	220
Siphonophora	2,196	3,543	5,943	3,055	4,185	6,137	3,723	4,356	4,142
Chaetognatha	1,346	2,834	2,955	1,259	4,813	2,420	2,346	3,128	2,638
Annelida	184	157	238	188	366	357	128	410	254
Calanoid Copepoda	12,762	38,733	32,069	18,704	30,395	20,078	13,439	24,916	23,893
Non-calanoid Copepoda	1,359	2,362	2,301	1,192	4,028	1,796	1,898	2,905	2,230
Ostracoda	1,974	2,559	2,633	3,515	6,069	607	550	1,937	2,480
Euphausiacea	1,338	2,440	4,541	1,673	3,139	1,662	1,893	1,788	2,309
Amphipoda	958	905	526	401	942	869	548	521	709
Decapod Crustacea	2,120	3,976	4,460	1,842	3,768	3,060	3,331	5,028	3,448
Pteropoda	486	945	1,361	546	1,360	446	1,049	1,378	946
Heteropoda	247	79	394	38	52	68	118	----------	124
Gastropod larvae	50	197	174	33	105	138	136	298	141
Pelecypoda	50	----------	74	177	----------	44	132	223	88
Thaliacea	11	157	202	464	1,308	668	146	372	416
Appendicularia	135	157	851	720	3,191	216	255	1,639	896
Fish larvae	234	236	269	292	366	692	171	----------	282
Fish eggs	96	79	31	90	314	25	21	112	96

[1] *Halosphaera viridis*, a phytoplankter.

The physical, chemical, and biological characteristics of each of the nine periods are discussed below. For the discussion the averages for each period are considered high or low relative to the overall average for the nine periods. A night sample of zooplankton was not taken in May 1958; thus, the counts of zooplankton for night collections are divided into eight rather than nine periods (table 4).

JUNE TO JULY 1957

This period was characterized by relatively high temperatures, low salinities, and a shallow isothermal layer. The average 0 to 60 m. temperature was 25.6° C. The 0 to 60 m. and 200 to 300 m. average salinities were 34.92‰ and 35.00‰, respectively, compared to the nine-period means of 34.97‰ and 35.08‰. The average depth to the top of the thermocline was 51.4 m. (fig. 8).

The average volume of zooplankton for day hauls equaled the nine-period mean of 20 cc./1,000 m.³ (fig. 9); the average night volume of 25 cc./1,000 m.³ was lower, however, than the eight-period mean of 37 cc./1,000 m.³ Most of the counts of groups of organisms were low (table 4); *Halosphaera*, Foraminifera, Amphipoda, and Heteropoda were exceptions. The abundance of calanoid Copepoda, which numerically make up about 59 percent of the total standing crop of zooplankton, was very low during this period.

AUGUST 1957

August 1957 appeared to be a transition period (fig. 7). The 0 to 60 m. salinity increased from 34.92‰ to 34.98‰, and the 200 to 300 m. salinity increased slightly from 35.00‰ to 35.02‰. The 0 to 60 m. temperature (26.0° C.) also increased. The depth of the isothermal layer (49.1 m.) decreased from the previous period.

The volume of zooplankton for the day hauls (18 cc./1,000 m.³) for this period was slightly less than the average for June to July 1957; however, the night volume (44 cc./1,000 m.³) showed a substantial increase. Radiolaria and calanoid Copepoda were more abundant in August 1957 than in any other period.

SEPTEMBER TO NOVEMBER 1957

Temperature and depth of the isothermal layer for this period were lower; salinities were higher than in the previous period. The average 0 to 60 m. temperature was 25.9° C. The depth to the top of the thermocline was 47.4 m. The 0 to 60 and 200 to 300 m. salinities were 35.14‰ and 35.11‰, respectively.

The average volumes and counts of zooplankton were high. Volumes for day (25 cc./1,000 m.³) and night (56 cc./1,000 m.³) samples were both higher than the corresponding averages (20 cc./1,000 m.³ and 37 cc./1,000 m.³) for all periods. Euphausiacea and Heteropoda were more abundant in this period than in any other.

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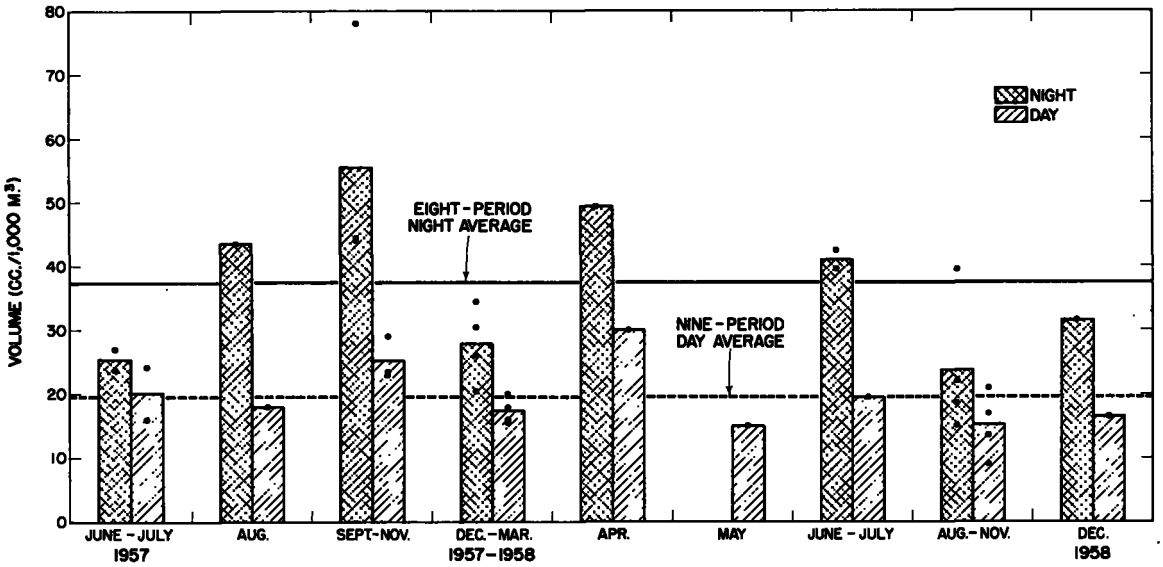

FIGURE 9.—Average volumes of zooplankton during nine periods at the IGY station.

DECEMBER 1957 TO MARCH 1958

Monthly changes of the measured properties from July to November 1957 were gradual; the change from November to December 1957, however, was abrupt. The 0 to 60 m. temperature dropped from an average of 25.9° C. in November 1957 to 24.6° C. in December 1957 (fig. 6A) and remained low, averaging 24.1° C. for December 1957 to March 1958 (fig. 8A). The monthly 0 to 60 m. salinity likewise changed considerably, dropping from 35.12‰ in November to 34.82‰ in December (fig. 6B). The December 1957 to March 1958 average was 34.92‰ (fig. 8B).

The 200 to 300 m. salinity (35.10‰) changed slightly (fig. 8C), but the depth to the top of the thermocline showed a considerable deepening from an average of 47.4 m. during September to November 1957 to 84.6 m. (fig. 8D) for this period.

The volumes of zooplankton declined markedly from the preceding period. The night volume dropped from an average of 56 cc./1,000 m.³ in September to November 1957 to 28 cc./1,000 m.³ The day volumes of zooplankton declined from 25 cc./1,000 m.³ to 17 cc./1,000 m.³ (fig. 9). Except for *Halosphaera*, Ostracoda, Pelecypoda, and Thaliacea the abundance of plankters was relatively low during this period.

APRIL 1958

Maximum and minimum values were recorded for the physical and chemical properties during April 1958 (figs. 6 and 8). The 0 to 60 m. temperature (22.8° C.) was the lowest recorded during the 19 months. The 0 to 60 m. salinity (35.14‰) equaled the September to November 1957 average, the highest average for the nine periods. The 200 to 300 m. salinity (35.18‰) was also the highest for the nine periods. The isothermal layer during this period was the shallowest (22.6 m.) of the nine periods.

The zooplankton showed marked differences from the preceding period. The day and night volumes of 30 cc./1,000 m.³ and 50 cc./1,000 m.³ for April were much higher than those for December 1957 to March 1958. With the exception of Pelecypoda, all of the organisms were more numerous than in the preceding period.

MAY 1958

In May the physical and chemical characteristics of the water differed markedly from those of April 1958. The 0 to 60 m. temperature increased from the low of 22.8° C. in April to 24.6° C. in May. The most important change, however, was in the 0 to 60 m. salinity, which decreased from 35.14‰ in April, the highest for the nine periods, to 34.78‰ in May, the lowest for the nine periods. The 200 to 300 m. salinity decreased slightly from 35.18‰ in April to 35.13‰ in May. These differences suggest that the major change from April to May was in the upper waters. The depth to the top of the thermocline (62.8 m.) was slightly greater than the nine-period mean (59.4 m.).

The average volume of zooplankton for the day hauls was 15 cc./1,000 m.^{3}, lower than that for any previous period.

JUNE TO JULY 1958

Except for a continued rise in temperature and a shallower isothermal layer, the changes during this period were not very great. The average 0 to 60 m. temperature was 25.5° C. The average 0 to 60 m. salinity increased to 34.86‰. The average 200 to 300 m. salinity declined further to 35.10‰. The average depth to the top of the thermocline was 49.8 m.

The night volumes of zooplankton for June to July averaged 41 cc./1,000 m.^{3} as compared to the eight-period average of 37 cc./1,000 m.^{3}, and the average day volume of 20 cc./1,000 m.^{3} was the same as the nine-period day average. Siphonophora, Annelida, Amphipoda, Thaliacea, and fish larvae were relatively abundant in this period.

AUGUST TO NOVEMBER 1958

Changes in temperature, salinity, and depth of isothermal layer continued. The 0 to 60 m. temperature reached its 1958 peak in this period with an average of 26.3° C. The average 0 to 60 m. salinity (34.92‰) increased over the preceding period (34.86‰). The average 200 to 300 m. salinity continued to decline to 35.00‰. This period and June to July 1957 had the lowest 200 to 300 m. salinities for the nine periods. The depth to the top of the thermocline deepened to an average of 74.0 m.

The low abundance of zooplankton was similar to the lows of June to July 1957, December 1957 to March 1958, and December 1958. Only the averages for Pteropoda and Pelecypoda were above the eight-period average.

DECEMBER 1958

This period was characterized by a marked decrease in temperature, rising salinities, and a progressively deepening isothermal layer. As in 1957, the 0 to 60 m. temperature underwent a large drop between November and December. For 1958 the decline was from 25.9° C. in November to 24.1° C. in December (fig. 6A). The 0 to 60 m. salinity of 35.07‰ continued to increase from 34.82‰ in July (fig. 6B). The 200 to 300 m. salinity (35.06‰) increased from the previous period. The depth to the top of the thermocline was 93.3 m.

The volume of zooplankton for December 1958 was again lower than the nine-period average. Except for seven groups (*Halosphaera*, Foraminifera, Ostracoda, Amphipoda, Heteropoda, Thaliacea, and fish larvae), however, the plankton during December 1958 was more abundant than in June to July 1957, December 1957 to March 1958, and August to November 1958.

COMPARISON BETWEEN PERIODS

A noticeable feature in the 19 months' observations was the dissimilarity of the hydrographic features for the same months of the 2 years. The 200 to 300 m. salinities for June to July were substantially lower in 1957 than in 1958, whereas the 0 to 60 m. and 200 to 300 m. salinities for August to November were higher in 1957 than in 1958. The depth to the top of the thermocline was shallower in the fall of 1957 than in the fall of 1958. The 0 to 60 m. temperatures reflected the seasonal fluctuations of high temperatures in summer and fall and low temperatures in winter and spring and so did not vary greatly between years for the same months.

Zooplankton was more abundant during the fall of 1957 than in the fall of 1958 (figs. 4 and 9). Previous studies of the distribution of zooplankton in Hawaii have indicated a lack of consistent seasonal change. In 1950 and 1951, volumes were significantly higher during early summer and midsummer than in late summer and fall (King and Hida, 1954). But in 1956, the standing crop of zooplankton was greatest in January, April, and September (Nakamura, 1967).

June to July 1957 and August to November 1958 were alike. Both had similar T-S curves (fig. 7), hence their temperature and salinity characteristics were similar (fig. 8). Both of these periods had low volumes of zooplankton (fig. 9). The day volume of zooplankton for June to July 1957 was equal to the nine-period mean while that for August to November 1958 was low.

December 1957 to March 1958 and May 1958 were also alike. Both had similar T-S curves (fig. 7). Both had low day volumes of zooplankton. A night volume was not available for May 1958.

The two periods (September to November 1957 and April 1958) that had high night and day volumes of zooplankton (fig. 9) also had high 0

to 60 m. and 200 to 300 m. salinities (fig. 8), but their temperatures were quite dissimilar (fig 8).

VARIATIONS OF ZOOPLANKTON AND SALINITY

Of great interest were the coincident variations in the night volumes of zooplankton with variations in the portions of the T-S curves with salinities >35.0‰. As shown in figures 7 and 9, increases or decreases in night volumes of zooplankton appeared with corresponding changes in the salinity. The T-S curves indicated a progressive invasion of high-salinity water in the upper surface layers from June to July 1957 to September to November 1957. The night volumes of zooplankton increased correspondingly during these same periods. In December 1957 to March 1958, less saline waters returned to the uppermost layer of the ocean and the volume of zooplankton dropped below that of the preceding period. Then in April 1958 high-salinity water again invaded the area, and the volume of zooplankton increased. During May 1958 the salinity maximum was about the same as in the previous period, but the surface water was less saline. A night volume of zooplankton was not available for this period. During the next two periods, June to July 1958 and August to November 1958, the occurrence of high-salinity waters decreased progressively. Corresponding decreases also were evident in the night volumes of zooplankton. Water of higher salinity returned again in the uppermost layer during December 1958 coincident with an increase in the night volume of zooplankton.

Thus, waters of high salinity appeared to sustain a greater biomass of zooplankton. The abundance of several groups of zooplankton fluctuated coincidentally with the night volumes and with salinity. These groups were Siphonophora, Chaetognatha, Euphausiacea, decapod Crustacea, and Pteropoda (fig. 10). Because of the correlation of the abundance of these zooplankters with water type, the possibility of finding endemic species appeared favorable. Sherman (1963) found certain species of calanoid Copepoda (Pontellidae) associated with, and thus useful as indicators of, waters of high salinity (North Pacific Central Water) in the Hawaiian area. These groups of zooplankton

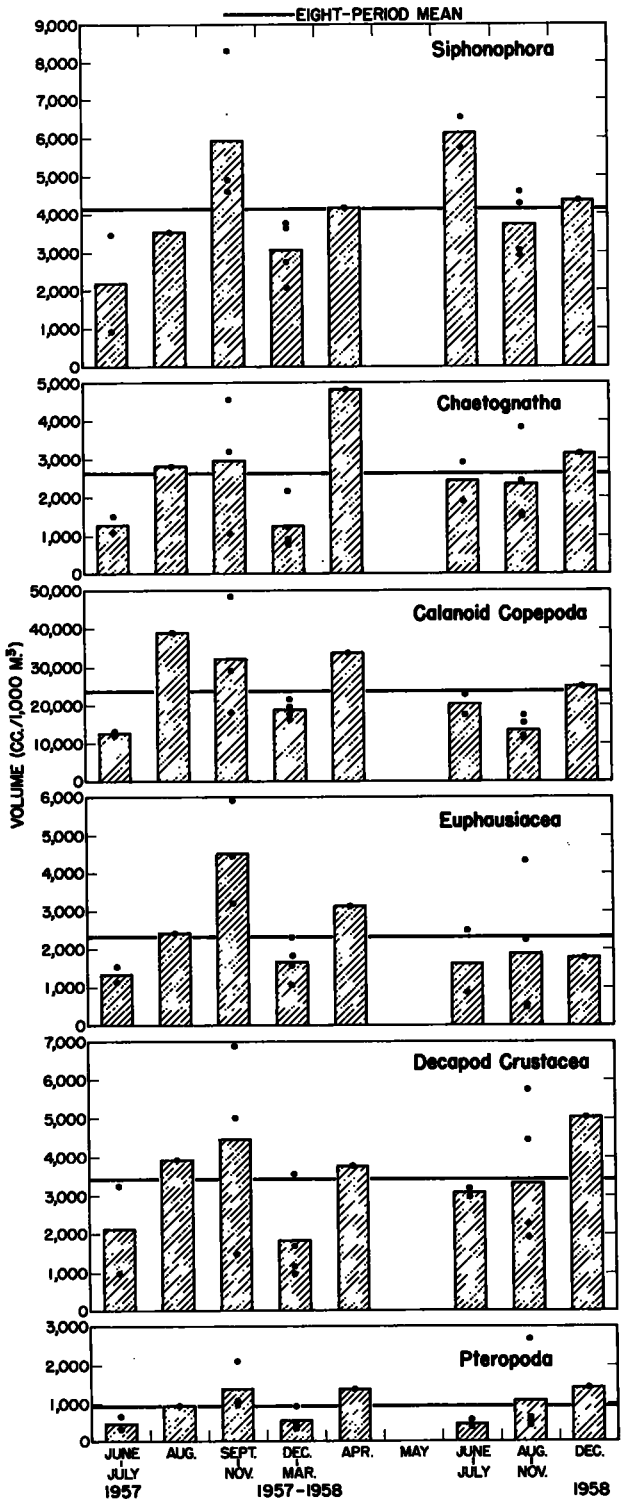

FIGURE 10.—Average abundance of six groups of zooplankton at night during eight periods at the IGY station.

may include other species possibly useful as indicators.

SUMMARY

1. Data on zooplankton and hydrography were obtained at lat. 21°10.3′ N., long. 158°19.0′ W. from June 1957 to December 1958. The station was visited once a month, and samples were taken once at highest tide and once at lowest tide. In June 1957, the station was occupied for 48 hours to obtain samples for studies of diel variation.

2. Volume of zooplankton from the 48-hour series conformed to the characteristic sinusoidal variation for the first day, but not for the second. A diatom that prevented drainage of moisture during determination of the volumes probably caused the high volumes during the morning of the second day. Variations in abundance were distinctly sinusoidal for Ostracoda, Euphausiacea, Pteropoda, and fish larvae. Variations in surface temperature were attributed to heating during the day and cooling during the night. Variations in the depth to the top of the thermocline were attributed to internal waves.

3. Correlations were significant and positive between day volumes of zooplankton and salinities at the surface and at 0 to 60 m., and for night volumes of zooplankton and salinities at 200 to 300 m. Positive correlations for night volumes of zooplankton and salinities at 0 to 60 m. and for day volumes and salinities at 200 to 300 m. were very close to the 5-percent probability. Correlations were significant and negative between both day and night volumes of zooplankton and depths to the top of the thermocline.

4. The 19 months were divided into nine periods, each period having a temperature-salinity curve different from the preceding and the following periods.

5. Salinities and depths to the top of the thermocline were dissimilar for the same months in 1957 and 1958. Night volumes of zooplankton were highest in the fall of 1957.

6. Variations in the night volumes of zooplankton coincided with variations in salinities $> 35.0‰$. As the salinity increased, zooplankton increased; as salinity decreased, zooplankton decreased. The abundance of Siphonophora, Chaetognatha, Euphausiacea, decapod Crustacea, and Pteropoda fluctuated coincidentally with the night volumes of zooplankton and with salinity.

ACKNOWLEDGMENT

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ADDITIONAL REFERENCES ON THE BIOLOGY OF SHRIMP, FAMILY PENAEIDAE [1]

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ABSTRACT

About one thousand references to shrimp are given. Citations are listed alphabetically by author. References include those on biology and fishing gear.

The Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex., is studying the commercial shrimp of the family Penaeidae that inhabit the Gulf of Mexico. As background for this research, Chin and Allen (1959) published literature references on shrimp biology. We now present about one thousand additional references to supplement that list. Most references contained in our report were published from 1958 through 1966, although we have included a few that were previously overlooked.

Many unpublished reports and theses concerning Penaeidae came to our attention while we were compiling the published citations. These unpublished reports are presented to indicate additional sources of pertinent information. Published and unpublished references are listed separately.

We have followed generally the procedure used by Chin and Allen (1959). References are listed alphabetically by the author's surname. Only references concerning shrimp of the family Penaeidae are listed, and the subject is limited primarily to shrimp biology. References concerning fishing methods and gear, however, are included because they are useful to fishery biologists. We made no special effort to obtain references to paleontological studies, the shrimp processing industry, or shrimp statistics, although the list contains some citations in those fields.

Additional exclusions from the lists of citations should be noted. We have not included literature published after 1966. Some articles that concern Penaeidae were not available to us for checking the accuracy of citation and have not been included. No attempt was made to include all brief notes on shrimp research and shrimp fisheries that appeared in CFR (Commercial Fisheries Review). These notes are cited in the CFR yearly index. Pertinent lead articles appearing in CFR, however, are included. Many Florida State Board of Conservation Special Mimeographed Reports contained pertinent but limited information on shrimp and were excluded. We often excluded popularized articles derived from more basic reports already cited in our list, abstracts that were followed by complete reports, and unpublished papers that were superseded by published versions. Some duplication of information, however, was unavoidable.

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FOOD, GROWTH, MIGRATION, REPRODUCTION, AND ABUNDANCE OF PINFISH, *LAGODON RHOMBOIDES*, AND ATLANTIC CROAKER, *MICROPOGON UNDULATUS*, NEAR PENSACOLA, FLORIDA, 1963–65

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ABSTRACT

The abundance, growth, age composition, food, migration, and reproduction of the two species were studied at two locations for each species from August 1963 to December 1965. The materials comprised 22 fish collections at each station, taken in about 500 hours of trawling.

The stomach contents of 3,577 pinfish and 2,520 Atlantic croakers indicated that pinfish are omnivorous and croakers carnivorous. Principal foods were vegetation, crustaceans, and polychaetes for pinfish and annelids, fish, and arthropods for croakers. Types of food in pinfish stomachs were similar at all sizes and seasons, but the relative amount of each type differed by season and size of fish. Foods in croaker stomachs differed at the two stations but were similar from year to year. The average food volume in the stomachs varied with time of year, location, and fish size. Volumes of food in stomachs of both species decreased when the fish moved from the estuary.

Length-frequency distributions can be used to estimate age in both species. Pinfish, and possibly croakers, form annuli on their scales. Growth of pinfish and Atlantic croaker varied from year to year.

Some fish of both species had developing gonads in the fall of their first year of life and may spawn. Both species migrate offshore in the fall to spawn. The fry and some adults return to the estuary in the winter and spring.

Abundance of pinfish and Atlantic croakers was highest in late spring and early summer. Pinfish at both stations and croakers at one station were less abundant in 1964 than in 1963 or 1965. Yearly differences in abundance of croakers were not large at the other location.

Pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogon undulatus*, are two of the most abundant species of fish in the Pensacola area and other estuaries in the Southeastern States. The life history of pinfish from areas other than Pensacola has been investigated by Reid (1954), Kilby (1955), Caldwell (1957), and others; and that for Atlantic croaker has been studied by Pearson (1928), Hildebrand and Cable (1930), Wallace (1940), Gunter (1945), Haven (1957 and 1959), and others. The purposes of the present study were to investigate the life histories of these species in the Pensacola Estuary and to contribute to the general knowledge of the biology of these fishes.

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DESCRIPTION OF THE STUDY AREA

The "Pensacola Estuary" (so termed for convenience) has an area of about 370 km.^{2}; it encompasses three bays (two of which are shown in fig. 1) and a sound. The estuary supports commercially harvested stocks of fish and shellfish.

Two stations in the lower estuary were selected for study of pinfish. The sandy bottom at both supports a dense growth of grasses—predominantly turtle-grass, *Thalassia testudinum*, and seagrass, *Ruppia maritima*. Station I is on the north side of Santa Rosa Sound across from Sabine Island, site of the Bureau of Commercial Fisheries Biological Field Station, Gulf Breeze, Fla.; station II is on the south side of Pensacola Bay. Average depth at mean low water is 3.0 m. at station I and

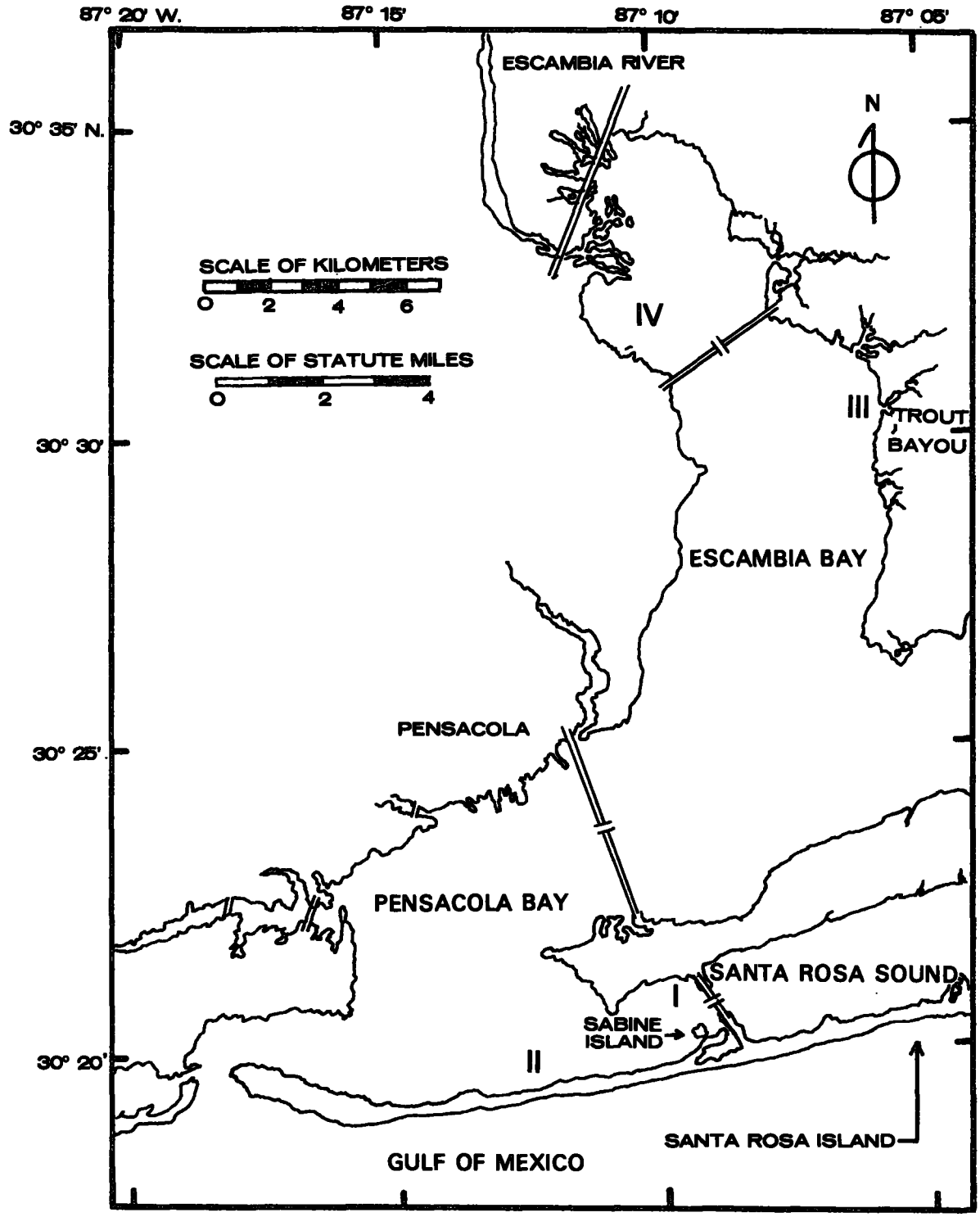

FIGURE 1.—Location of sampling stations in the Pensacola Estuary for pinfish (I and II) and Atlantic croaker (III and IV).

2.5 m. at station II. Salinities at both stations ranged from 4 to 31 p.p.t. and averaged 23 p.p.t. at station I and 24 p.p.t. at station II. Water temperatures were similar at both stations, ranging from 9° to 30° C. and averaging 23° C.

Two locations in the upper estuary were selected for study of Atlantic croakers—station III, off the eastern shore of Escambia Bay, near Trout Bayou, and station IV, off the western shore of the bay. The bottom at both is predominantly mud; attached vegetation is lacking, but station III has isolated oyster reefs. Average depth at mean low water is 2.5 m. at station III and 2.0 m. at station IV. Salinities ranged from 0 to 29 p.p.t., average 15 p.p.t., at station III and from 0 to 27 p.p.t., average 12 p.p.t., at station IV.

MATERIALS AND METHODS

Collections were made with a 5-m. otter trawl of 12-mm. bar mesh. This trawl is the standard "try net" used by commercial shrimpers in Pensacola Bay to find commercial quantities of shrimp. The trawl was pulled behind the 11-m. research vessel *Dolphin* at about 2.5 knots.

All stations were visited 22 times from August 1963 to December 1965; usually 10 trawl hauls (30 minutes) were made at each Atlantic croaker station and 30 hauls (15 minutes) at each pinfish station. Trawling usually began in the middle of the month and lasted 7 days (not necessarily consecutive). The number and duration of hauls were selected to give a reliable estimate of fish abundance. In periods when fish were not abundant the number of trawl samples was reduced to less than half that during periods of abundance.

Treatment of both species after capture was similar. On the boat they were counted, measured to the nearest millimeter of standard length, and whenever possible 50 fish from each 25-mm. size group were preserved in a mixture of 4 percent formaldehyde and sea water of 16 p.p.t. salinity. Fish were slit open to preserve innards (including stomach and gonads). At the laboratory, preserved fish were measured for length and weight (to the nearest millimeter and 0.01 gram) and stomachs and scale samples were removed.

Confidence intervals were computed for the number of fish caught per trawl-haul and on the average length of the fish. Mention of significant differences indicates that confidence intervals, 95 percent confidence coefficient, do not overlap.

Stomach contents of fish captured at the same time were combined by length of the fish—14 to 75 mm. or >75 mm.—and stored in 70 percent ethanol. After identifying and sorting the contents, I blotted them dry and determined their liquid displacement.

Discussion of the volume of stomach contents includes all of the contents but discussion of the composition excludes unidentifiable material; which represented 8.8 percent of the 205.8 ml. of food from 3,577 pinfish stomachs and 25.2 percent of the 58.4 ml. of food from 2,520 Atlantic croaker stomachs. The unidentifiable component of the stomach contents included small particles of inorganic and organic detritus and food digested beyond recognition. Reid (1954) also found large amounts of unidentifiable material in croaker stomachs.

Ages were determined from length-frequency distributions and by examination of scales. The scales were predominantly from fish at the size range where length-frequency distributions indicated a change in age. The scales were taken from the area above the lateral line behind the operculum, stored between sheets of paper, and examined under a monocular microscope. The distances from focus of the scale to the annulus and to the margin of the scale were measured to the nearest 0.1 mm. with an ocular micrometer.

The spawning season extends throughout the winter (about November to March for pinfish and November to February for croakers). In assigning ages to these fish, I used January 1 of the year following the winter of hatching as the first birthday.

I used two methods to study the growth. First, I used the differences in average lengths between consecutive trawling periods to compute the average daily increases in length. Second, I used measurements of scales from yearling pinfish to compute growth increments; increases in length after annulus formation were determined for each sampling date and used to derive daily growth for each season.

To discover movements before spawning, I clipped fins of 26,980 pinfish and 5,269 Atlantic croakers. Fish from different localities were marked differently by removal of either one or both pelvic fins. After the marking, the fish were kept in a tank of circulating water on the boat

until the next trawl-haul was completed, and only fish that seemed healthy were released. The area of release was not fished again for at least 15 minutes. Fish movement could be noted if fish fin-clipped at one station were recaptured at any of the other three stations or at other locations sampled sporadically. I also marked 284 pinfish by attaching an Atkins tag in front of the dorsal fin with nickel wire.

I estimated numbers of eggs in ovaries by measuring the volume of eggs in both ovaries (after most ovarian tissue had been removed) and dividing that value by the average volume of an egg as estimated from measurement of 25 eggs.

PINFISH

Pinfish are one of the dominant animals in the fauna of vegetated areas in the lower Pensacola Estuary. Therefore, I investigated the seasonal and annual change in the food, growth, migration, reproduction, and abundance at two locations from August 1963 to December 1965.

FOOD

Pinfish were omnivorous feeders on the grass flats where stations I and II were located. Gunter (1945) and Reid (1954) on the Gulf of Mexico Coast and Linton (1904) on the east coast of the United States found a large variety of food organisms in pinfish stomachs. I identified 10 phyla of animals and a wide variety of vegetation (including diatoms, filamentous algae, and vascular plants). The type of food varied with season and fish size (table 1), but not by station.

Vegetation contributed 40.6 percent of the total volume of identifiable items (including sand) in the stomachs. It was the dominant food in the summer and fall; the amount usually increased in late spring or early summer and decreased in the late fall. Diatoms were most important in fish less than 76 mm. long, and filamentous algae and vascular plants in larger fish.

Crustaceans, polychaetes, and chordates were dominant in pinfish stomachs in the winter and spring. Small pinfish usually contained a higher total number and volume of small crustaceans than large pinfish. The crustaceans were mainly amphipods, copepods, crabs, cyprids, isopods, mysids, and shrimp. Chordates—amphioxus and (secondarily) fish—were most abundant in large fish. Other animals eaten in smaller amounts were brachiopods, bryozoans, chaetognaths, echinoderms, mollusks, and nemerteans.

The mean volume of food in pinfish stomachs was highest during the summer and early fall (table 2). The increase in the volume usually began in May or June for both size groups of fish and came with increase in ingestion of vegetation. The volume decreased in the fall as fish became more carnivorous. In the fall most fish over 90 mm. long leave the estuary. Amounts of food in the stomachs decrease during the spawning season, as is common in many species of fish.

The mean volume of food in pinfish stomachs was generally low and nearly constant from late fall until late spring, except for a short-term increase in February, when large numbers of caprellid amphipods and polychaetes were found in stomachs of small fish.

TABLE 1.—*Percentage of total volume contributed by differen items in pinfish stomachs collected in the lower Pensacola Estuary at stations I and II in different seasons, 1963–65*

Items in stomachs	Fish length class, season, and number of stomachs [1]								
	< 76 mm.				76–173 mm.				All (3577)
	Spring (537)	Summer (887)	Fall (570)	Winter (122)	Spring (184)	Summer (683)	Fall (575)	Winter (19)	
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Crustaceans	58.3	2.8	21.7	44.8	8.7	4.6	5.6	24.9	26.9
Polychaetes	17.3	1.0	2.9	43.4	8.0	4.0	4.0	19.4	9.9
Chordates	3.1	1.5	1.1	10.8	12.5	2.0	2.9	31.3	6.6
Vegetation	4.6	87.2	66.5	.9	21.9	66.4	56.6	23.1	40.6
Sand	12.9	6.7	6.6	.0	44.4	18.9	29.5	.2	13.8
Other [2]	8.8	.8	1.2	.1	4.5	4.1	1.4	1.1	2.2

[1] Numbers of stomachs from both stations are shown in parentheses.

[2] Other items include brachiopods, bryozoans, chaetognaths, echinoderms, mollusks, and nemerteans.

TABLE 2.—*Average volume of stomach contents of small and large pinfish collected in the lower Pensacola Estuary at stations I and II in the months of sampling, 1963–65*

Month	Fish length class			
	<76 mm.		76–173 mm.	
	Stomachs Examined	Average contents	Stomachs Examined	Average contents
	No.	*Ml.*	*No.*	*Ml.*
January	32	0.01	1	0.07
February	90	.05	18	.08
March	6	.01	2	.08
April	341	.01	111	.07
May	190	.01	71	.11
June	326	.02	174	.11
July	296	.03	214	.12
August	265	.06	295	.14
September	183	.03	239	.07
October	228	.04	289	.08
November	159	.01	47	.03

AGE AND GROWTH

Pinfish were aged by using length-frequency data and by examination of scales. Length frequencies have been used to age pinfish (Caldwell, 1957) but scales have not. Pinfish from the two stations were of similar lengths; therefore, length-frequency data for the stations were pooled (fig. 2). The bimodal length-frequency distribution indicates at least 2 year-classes of pinfish.

Average length of pinfish at annulus formation, as determined by scale measurements, was similar to the average length of fish measured in early spring. Most of the annuli formed in April of both 1964 and 1965. The percentage of yearling fish that showed an annulus in different months in 1964 and 1965 (data combined) were as follows (number of fish in parentheses): January—12 percent (57); February—13 percent (85); March—0 percent (2); and early May—100 percent (42). Back-calculation of fish lengths showed that the 1963 and 1964 year classes formed a year-mark at average lengths of 61 and 78 mm., respectively. Fish from these year classes were at this size as yearlings in March or April. The average length of fish entering their third year of life was 127 mm. (15 fish) at the time of annulus formation.

The average size of pinfish varied during the different years (table 3). Yearly differences in average size result from a number of factors such as differences in hatching time and growth rate. Standard lengths of fish caught by trawling and seining during the study were 13 to 152 mm.; fish

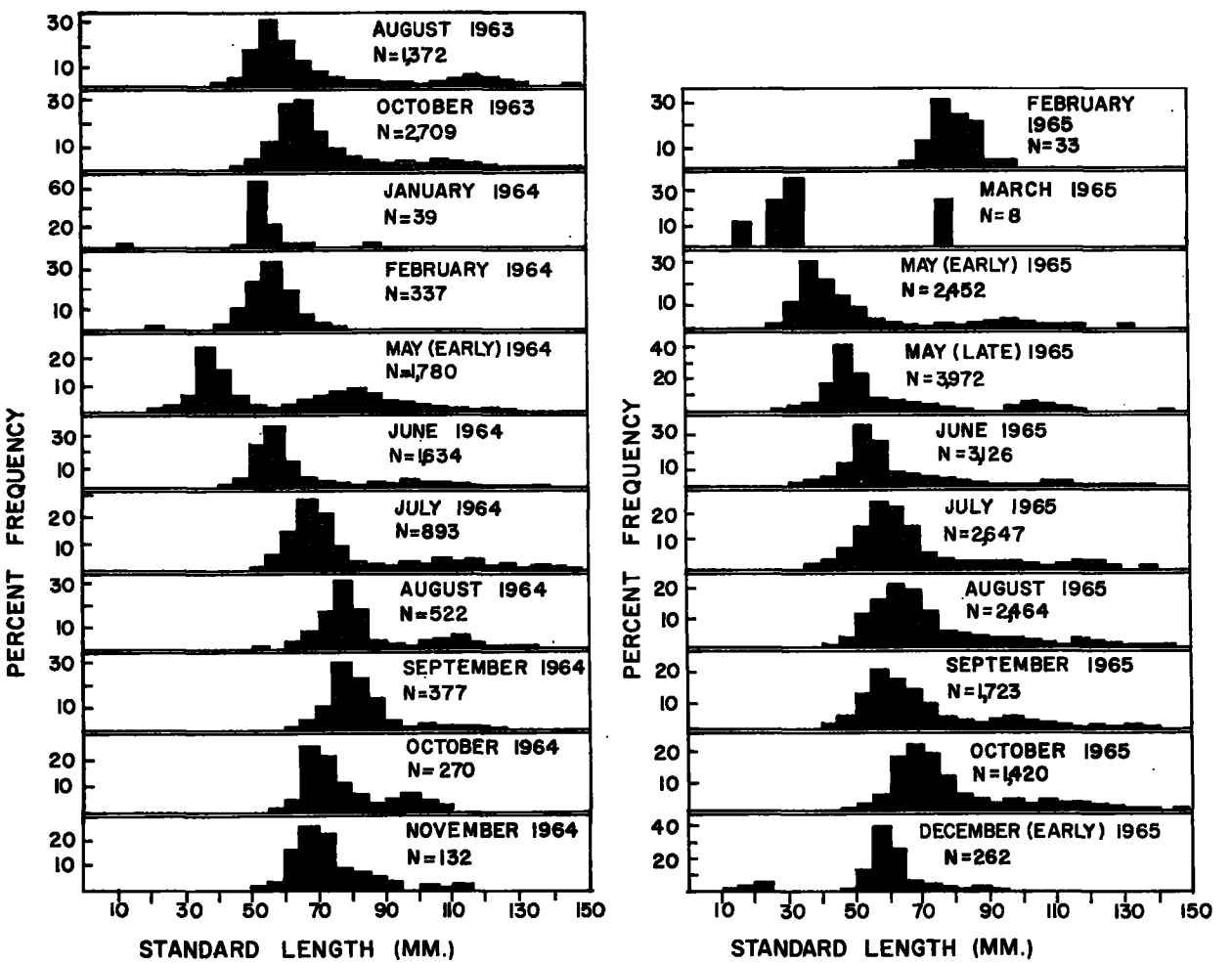

FIGURE 2.—Length-frequency distribution of pinfish caught in the lower Pensacola Estuary at stations I and II, 1963–65.

TABLE 3.—*Standard lengths of pinfish of age-groups 0, I, and II in the lower Pensacola Estuary at stations I and II, 1963–65*

Date	Age-group 0			Age-group I			Age-group II		
	Fish	Length		Fish	Length		Fish	Length	
		Average	Range		Average	Range		Average	Range
1963	*Number*	*Mm.*	*Mm.*	*Number*	*Mm.*	*Mm.*	*Number*	*Mm.*	*Mm.*
August 30–September 6	1,316	60	44–102	56	118	105–145	0		
October 29–November 1	2,642	67	47–107	67	117	107–145	0		
1964									
January 10–15	1	14		38	47	43–83	0		
February 28–March 3	1	22		336	56	43– 79	0		
May 12–14	1,008	39	21– 60	771	82	61–123	1	128	
June 29–July 1	1,567	57	42– 79	65	100	81–130	2	132	129–136
August 3–5	820	68	52– 93	62	109	91–140	2	136	136–137
August 31–September 2	438	76	50– 94	84	115	96–133	0		
September 28–30	352	80	60–101	25	112	102–128	0		
October 30–November 3	270	77	59–109	0			0		
November 23–25	132	72	53–110	0			0		
1965									
January 12	1	30		0			0		
March 3	0			33	81	69– 97	0		
March 29	6	28	19– 32	2	78	77– 79	0		
May 6–12	2,369	42	25– 60	82	96	76–116	1	134	
June 1–3	3,917	48	28– 78	53	102	77–111	2	137	136–138
June 25–29	3,098	54	33– 94	21	112	97–130	7	136	131–143
August 2–4	2,623	59	35–105	22	118	113–125	2	136	135–136
August 30–September 1	2,414	64	42–109	49	120	110–137	1	141	
September 22–24	1,706	68	45–110	17	123	113–139	0		
October 25–27	1,383	71	49–116	37	121	112–146	0		
December 6–8	8	20	14– 22	254	60	47– 92	0		

caught at the sampling stations were 14 to 146 mm. long.[1]

Pinfish growth rates computed from changes in lengths between consecutive trawling periods varied with age group and season. Daily increase in length averaged 0.19 mm. for 0-group pinfish and 0.12 mm. for yearlings. Growth of both age groups slowed as the seasons progressed from spring to winter. Daily increase in length of 0-group pinfish averaged 0.32 mm. in the spring, 0.23 mm. in summer, and 0.01 mm. in fall; yearling pinfish averaged 0.32 mm. in the spring, 0.21 mm. in summer, −0.04 mm. in fall, and −0.02 mm. in winter. Caldwell (1957) also observed maximum growth in the spring and negligible growth in the fall and winter.

Annual growth rate of yearling pinfish, estimated from increase in length after annulus formation, was closely similar to that based on increase in measured lengths, but seasonal growth rates determined by the two methods differed. Annual increase in length computed from scale measurements averaged 0.14 mm. per day, and seasonal increases averaged 0.12 mm. per day in the spring, 0.14 mm. in the summer, 0.20 mm. in the fall, and 0.09 mm. in the winter.

[1] Standard length=0.85 fork length or 0.78 total length on the basis of measurements of 100 fish, 44 to 101 mm. long.

MIGRATION AND REPRODUCTION

Limited data on estuarine movements of pinfish were obtained from recaptures of fin-clipped or tagged fish. Of 26,980 pinfish fin-clipped, 234 (0.87 percent) were recaptured at the area of original capture during the trawling period in which they were released and only 47 (0.17 percent) were recovered 1 month or more after marking. There could be several reasons for the low recapture rates. The proportion of the population marked was small, the marking mortality was high, or unmarked fish from other areas were moving in. Of the 47 fish recovered 1 month or more after marking, 39 were caught at the station of release, and eight had moved either from station I to station II or from station II to station I (five did so in the 3 principal months of the spawning migration—August, September, and October). Of 284 pinfish tagged in April 1964, two were recaptured—one in July about 125 m. from where it was tagged and the other in October about 3 km. closer to the mouth of the bay.

On the basis of results of trawling and seining, I believe that most pinfish remain over the grass flats where they live in the spring until they migrate out of the estuary in late summer and fall. Most appear to move very little in the summer, but a few may wander over the grass flats. Fish

may congregate in response to abundance or scarcity of food during this time but schools are not formed.

At the start of the spawning migration into the Gulf of Mexico, however, the pinfish school in large numbers. These schools seem to consist of fish of the same age. Large numbers of pinfish captured in Chesapeake Bay in October, as noted by Hildebrand and Schroeder (1927), probably were schools of seaward migrants. Aggregations of pinfish have also been seen in the Gulf of Mexico (Springer, 1957). In the late winter and spring, I have observed schools of pinfish in Santa Rosa Sound, Fla., that were probably returning from the Gulf of Mexico. Most of these fish were in their second year of life. Few fish live to reenter the estuary in their third year.

The stage of gonad development before migration varied. In most years, maturation of gonads probably takes place during the migration or while the fish are at or near the offshore spawning site. In October 1965, when most fish over 80 mm. were mature enough to permit determination of sex, the gonads ranged from the late stage 1 to the late stage 3 of Homans and Vladykov (1954)—gonads growing in size; yellow, opaque eggs microscopic to visible, and testes pinkish to flesh-colored or white and slightly distended. None had gonads that would produce milt or eggs when pressed (stage 4 or 5). Because the examination of scales showed that most fish under about 110 mm. were in their first year of life, it is likely that some 0-group fish and all yearling pinfish spawn.

Eight pinfish 111 to 152 mm. long had ovaries with eggs that were mature enough for counting; eggs in smaller fish were too small to count accurately. The diameters of eggs were 0.09 to 0.66 mm. (average 0.38) and the estimated numbers of eggs were 7,700 to 39,200 (average 21,600). Caldwell (1957) examined a pinfish 157 mm. long which had an estimated 90,000 eggs that averaged about 0.5 mm. in diameter.

ABUNDANCE AT THE SAMPLING STATIONS

Pinfish are present in moderate numbers in the deeper parts of Pensacola Bay in the summer; they are most abundant in the southern part of the estuary in extensive flats covered with turtle grass. Reid (1954) and Kilby (1955) also observed that pinfish were most numerous in vegetation along the Gulf Coast of Florida. Pinfish are distributed unevenly on the flats, as they tend to aggregate in response to the environment—concentrations of food especially attract them.

Despite the wide confidence limits on the average number of fish caught, seasonal trends are clearly evident (table 4). Because the periods of maximum and minimum abundance, and monthly changes in

TABLE 4.—*Pinfish caught per 15-minute trawl-haul in the lower Pensacola Estuary, 1963–65* [1]

Date	Station I			Station II			Averages both stations
	Average	Confidence interval 95 percent	Range	Average	Confidence interval 95 percent	Range	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
1963							
August 30–September 6	312	183–441	5–791	66	21–112	6–219	214
October 29–November 1	66	35– 96	0–253	59	48– 70	9–145	62
1964							
January 10–15	1	0– 3	0– 23	[2] 0	[2] 0– 0	0– 1	1
February 28–March 3	4	1– 7	0– 40	8	0– 16	0–111	6
May 12–14	19	11– 28	0– 97	40	26– 54	2–136	30
June 29–July 1	63	11–114	1–521	110	65–155	1–412	86
August 3–5	11	4– 18	0– 77	19	10– 28	0– 95	15
August 31–September 2	14	9– 19	0– 45	4	3– 5	0– 10	9
September 28–30	10	6– 14	0– 40	3	1– 4	0– 20	6
October 30–November 3	6	3– 10	0– 33	3	1– 4	0– 9	4
November 23–25	4	1– 7	0– 43	1	0– 1	0– 4	2
1965							
January 12	0			[2] 0	0– 1	0– 1	[2] 0
March 3	1	0– 2	0– 2	6	0– 18	1– 23	3
March 29	1	0– 4	0– 5	[2] 0	0– 1	0– 1	1
May 6–12	58	32– 84	0–208	29	12– 47	0–214	44
June 1–3	120	82–157	0–299	80	49–112	0–326	100
June 25–29	142	98–186	4–409	231	177–286	3–541	186
August 2–4	99	61–138	3–325	144	75–212	0–776	122
August 30–September 1	40	26– 52	1–123	92	52–132	0–469	66
September 22–24	22	15– 29	1– 83	68	45– 92	0–218	45
October 25–27	19	13– 26	0– 71	30	18– 41	0–137	25
December 6–8	8	3– 12	0– 51	2	1– 2	0– 6	5

[1] 30 trawl-hauls were made at each station on each visit, with the following exceptions (number of hauls in parentheses): Aug. 30–Sept. 6, 1963—station I (15), station II (10); Jan. 12, Mar. 3, and Mar. 29, 1965—each station (5).

[2] Less than 0.5.

abundance, were similar from year to year, I assume that average catch gives a reasonably good estimate of general abundance.

Pinfish young (O-group) and older migrants returning to the estuary began to arrive on the grass flats at both stations in late November and early December. Trawling did not capture young fish in numbers indicative of their actual abundance but seining caught large numbers of them near both stations. The migration continued until the population had reached a maximum by late June. The month that young first appear seems to depend on conditions offshore, because salinity and temperature changes in the estuary show no relation to the time of migration. Progressively fewer fish were captured after June because of natural mortality and emigration.

Pinfish abundance changed from year to year. If catch in August (a month fished in each of 3 years) is used as an indicator of yearly changes in abundance, pinfish were significantly less plentiful in 1964 than in 1963 or 1965. Pinfish were most numerous at station I in 1963 and at station II in 1965. The number of fish caught in the winters of 1963–64 and 1964–65 did not differ from November to February at station I and November through April at station II.

The numbers of fish caught at the two stations at each sampling time were similar, differing significantly only in August and September of each of the 3 years. This period marks the start of migration out of the estuary; significant changes in abundance might, therefore, be expected if the fish left one station earlier than the other.

ATLANTIC CROAKER

Atlantic croakers are one of the dominant fish in the upper Pensacola Estuary. Therefore, I investigated seasonal and annual change in the food, growth, migration, reproduction, and abundance at two locations from August 1963 to December 1965.

FOOD

Atlantic croakers are carnivorous (table 5). The animal food in the present collections included five phyla and numerous species. Vegetation and sediments in some stomachs were probably taken incidentally while fish were capturing animal food.

TABLE 5.—*Percentage of total volume contributed by different items in Atlantic croaker stomachs collected in the upper Pensacola Estuary at stations III and IV in different seasons, 1963–65*

Items in stomachs	Fish length class, season, and number of stomachs [1]								
	<76 mm.				76-173 mm.				All lengths (2,520)
	Spring (488)	Summer (222)	Fall (63)	Winter (230)	Spring (317)	Summer (981)	Fall (162)	Winter (7)	
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Arthropods	25.8	3.2	4.1	20.6	26.5	28.0	7.0	8.1	14.3
Mollusks	2.3	3.3	.0	.1	8.4	9.2	1.7	.0	3.5
Annelids	43.4	74.2	92.6	51.6	26.4	40.0	66.9	89.5	61.5
Nemerteans	.6	1.4	.0	.0	.1	.2	.3	.0	.3
Fish	19.9	11.9	.9	27.1	35.1	17.0	17.3	.0	15.9
Vegetation	1.5	1.5	.0	.2	1.8	4.3	4.2	1.3	2.0
Sediments	6.5	4.5	2.4	.4	1.7	1.3	2.6	1.1	2.5

[1] Numbers of stomachs from both stations are shown in parentheses.

Annelids were the major food except in large fish in the spring, when fish were dominant. Pearson (1928), who collected along the Gulf Coast, and Roelofs (1954), on the Atlantic Coast, found that annelids were dominant and that the other foods listed in table 5 were present in the stomachs of young croakers.

Fish were most common in Atlantic croakers over 75 mm. long. At station III, fish were most plentiful in stomachs in the spring and summer. At station IV, fish were most abundant in the winter in croakers less than 76 mm. long and in the spring in croakers over 75 mm.

Arthropods, chiefly crustaceans, were most plentiful in small fish in the winter and spring and in large fish in the spring and summer. The most important crustaceans were copepods, amphipods, isopods, mysids, shrimp, and crabs; larger forms were most common in stomachs of large fish. Insects—mainly tendipedids, dytiscids, and anisopterans—made up 67 percent of the arthropods in stomachs collected at station IV after heavy runoff in the spring.

Mollusks and nemerteans were minor constituents in the stomachs of Atlantic croakers. Mollusks were most plentiful in stomachs of large fish in the spring and summer.

The volume of food in croaker stomachs was greatest in the winter and spring; average for 768 fish under 76 mm. long was 0.02 ml. and for 324 fish over 75 mm. long, 0.04 ml. Food volumes decreased in the summer and fall; for 285 fish less than 76 mm. long the average volume was 0.01 ml. in both summer and fall, and for fish longer than

75 mm., the average was 0.03 ml. in the summer (981 fish) and 0.01 ml. in the fall (162 fish).

AGE AND GROWTH

I determined the age of Atlantic croakers by using length-frequency data. Fish from the two stations were of similar lengths, except for some segregation by size according to salinity (see next paragraph). Length-frequency data for the stations were, therefore, pooled (fig. 3). The data indicated that only 18 of 19,107 croakers (less than 0.1 percent) were in their second year of life.

Scales may be suitable for age determination of Atlantic croakers from the study area, but this method was unacceptable for Lake Pontchartrain fish (Suttkus, 1955). In the Pensacola Estuary, 6 of 201 Atlantic croakers had what may have been an annulus on their scales. The age of fish as indicated by scales conformed to that indicated by length-frequency data.

Changes in the size distribution of Atlantic croakers within this estuary occur when the larger fish move to areas of higher salinity. A faster growth rate in more saline waters would accentuate this size difference. In June 1964, 620 croakers averaged 70 mm. at station IV, and 1,290 averaged 76 mm. long at station III; in collections 8 and 12 miles below station III, 283 fish averaged about 94 mm. Length differences were still apparent in July. Average lengths were 90 mm. at station IV (149 fish), 91 mm. at station III (742 fish), and 98 mm. 12 miles below station III (155 fish).

The average size of Atlantic croakers varied during the different years (table 6) as a result of differences in hatching time and growth rate. In 1965, fish arrived in the estuary earlier than in 1964;

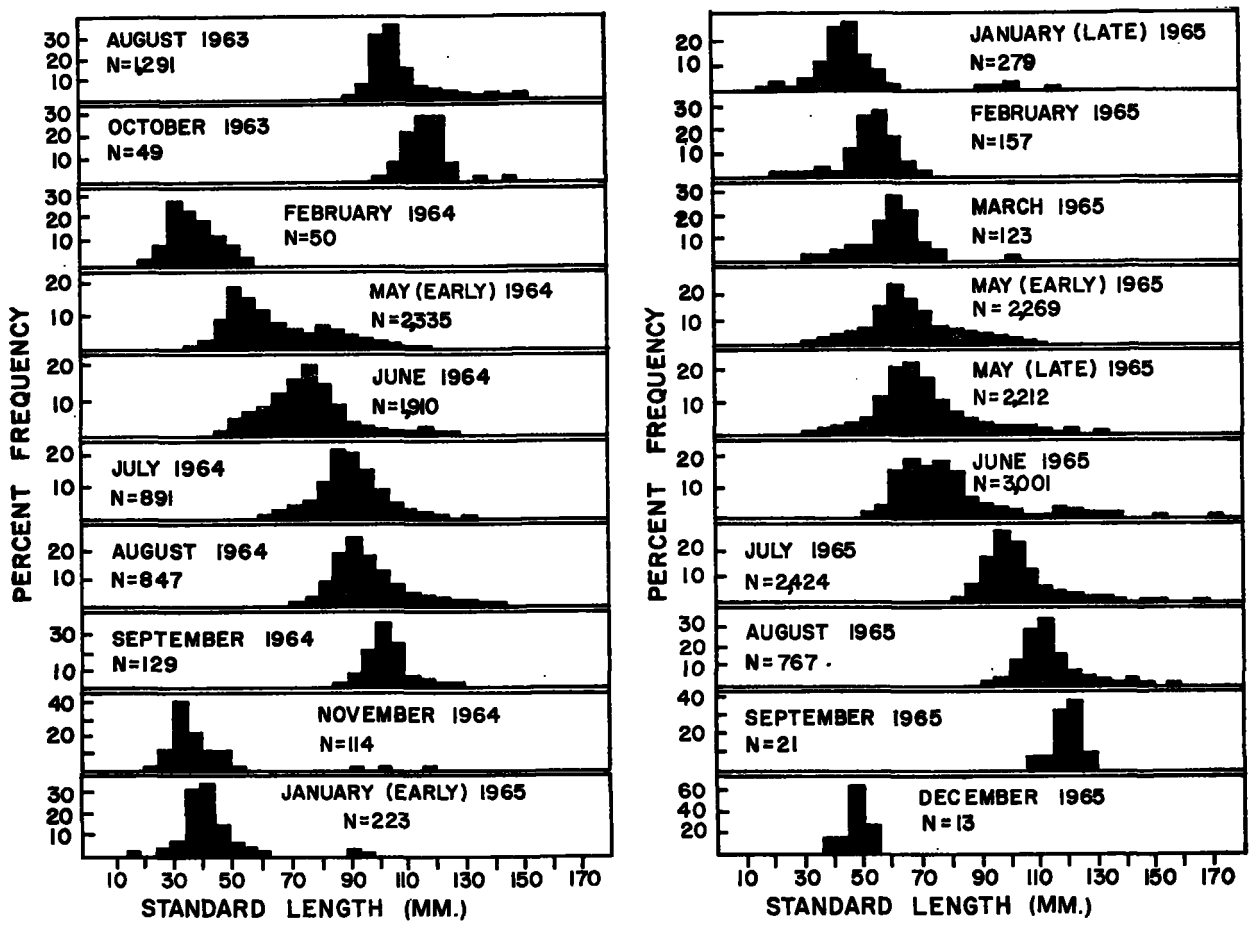

FIGURE 3.—Length-frequency distribution of Atlantic croakers caught in the upper Pensacola Estuary at stations III and IV, 1963–65.

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TABLE 6.—*Standard lengths of Atlantic croakers of age-groups O and I in the upper Pensacola Estuary at stations III and IV, 1963–65*

Date	Age-group 0			Age-group I		
		Length			Length	
	Fish	Average	Range	Fish	Average	Range
1963	*Number*	*Mm.*	*Mm.*	*Number*	*Mm.*	*Mm.*
August 22–29	1,291	107	91–152	0		
October 21–24	49	117	103–146	0		
1964						
January 6–14	2	32	24– 40	0		
February 24–27	50	38	20– 55	0		
May 5–11	2,335	65	35–117	0		
June 22–25	1,909	75	45–128	1	166	
July 27–30	891	91	61–131	0		
August 24–27	847	94	70–140	0		
September 21–24	129	102	86–125	0		
October 26–29	0			0		
December 8–10	111	35	24– 50	3	105	94–118
1965						
January 5–7	220	41	17– 60	3	93	91– 96
January 26–28	274	45	15– 64	5	102	94–118
February 23–March 2	157	54	21– 74	0		
March 22–31	122	61	30– 79	1	112	
May 3–7	2,269	67	34–113	0		
May 25–28	2,211	68	34–123	1	132	
June 21–24	2,999	74	51–136	2	163	153–173
July 26–30	2,422	99	68–151	2	164	161–168
August 24–27	767	111	93–155	0		
September 20–21	21	118	106–129	0		
December 1–2	13	47	38– 53	0		

therefore, they were larger in the winter, and from January through August grew at a faster rate (0.30 mm. per day in 1964, 0.36 mm. per day in 1965) so that in August they averaged 17 mm. longer than in 1964. Growth was greatest in the spring in 1964 and in the summer in 1965, and maximum growth was in July in both years (0.60 mm. per day).

MIGRATION AND REPRODUCTION

Migrations of Atlantic croakers are extensive. In December and January the young begin to enter the estuary from spawning grounds in the Gulf of Mexico and move to areas of low salinity. Haven (1957) noted that these fish move up the estuary in the salt-water "wedge" near the bottom. Two days of trawling (February 10–11, 1964) at all depths near the mouth of the Pensacola Estuary, however, caught no young croakers.

Atlantic croakers of age-group O appeared earlier and were more abundant at station IV in the years when estuarine water temperatures were relatively high in November and December. The average temperatures in November–December were: 1963—14.0° C., 1965—16.4° C., and 1964—19.2° C. In the winter of 1963–64 the first young-of-the-year croakers were caught in early January. In the winter of 1964–65 and 1965–66 they appeared in late November and early December (in the greater numbers in the winter of 1964–65). Young fish appeared first and in greatest abundance in areas of low salinity (station IV). They moved to areas of higher salinity as they grew and appeared in the lower estuary (stations I and II) in late spring. Fish caught at stations I and II were never as small as fish captured in the upper estuary near the beginning of the fry migrations.

Of 5,269 fin-clipped Atlantic croakers only 6 (0.1 percent) were recaptured, and only 2 of these had been marked at least 1 month before recapture. None had left the area of marking.

The migration of Atlantic croakers out of the estuary begins in late summer and ends before November. All fish probably leave the estuary; no croakers have been captured after the period of gulfward migration until the newly hatched fish enter the estuary.

Pearson (1928), Suttkus (1955), and Roithmayr (1965) found that, along the Gulf Coast, Atlantic croakers spawn at the end of their second year of life. In the Pensacola Estuary, most croakers had developing gonads in the fall of their first year of life. Most females and males examined had well-developed gonads (stage 2 or 3 of Homans and Vladykov, 1954). Although it is possible that the developing eggs are retained, these croakers may spawn in their first year of life.

Ovaries of 18 croakers, 101 to 145 mm. long,

caught in the fall of 1963, near the end of their first year of life, had an average of 41,200 eggs. The diameter of eggs was 0.02 to 0.72 mm. and averaged 0.34 mm. Hildebrand and Cable (1930) indicated that a mature egg probably has a diameter less than 1 mm. The eggs in the large yellow ovaries had fat globules.

ABUNDANCE AT THE SAMPLING STATIONS

Atlantic croakers are most abundant in low-salinity areas in the Pensacola Estuary. Young (O-group) enter the estuary in the winter and spring and move out in the fall. Fish in the estuary are rarely more than 10 months old.

Monthly changes in abundance (table 7) are caused primarily by migrations and, to a lesser extent, by natural mortality. In the winter young croakers move rapidly from the Gulf to the upper estuary; catches were largest at the station of lowest salinity. The number of fish increases to a maximum in May or June. Yearly differences in abundance were small at station III but croakers were most numerous at station IV in 1965.

SUMMARY

Life histories of pinfish and Atlantic croaker in the Pensacola Estuary were studied from August 1963 to December 1965. Their food, growth, age composition, migrations, reproduction, and abundance were studied from fish collected at intervals of about 1 month for 2½ years. Each species was sampled 22 times at each of two stations.

Feeding, migrations, and other aspects of the biology of pinfish from the Pensacola Estuary change seasonally. They spawn in the Gulf of Mexico in winter. Young and adults enter the estuary in the winter and spring where they congregate on grass flats and feed primarily on animals—crustaceans, polychaetes, and chordates—and attain maximum abundance in June. From June until the fall migration pinfish apparently move only short distances over the grass flats and are primarily herbivores. The amount of food in the stomachs is at its highest level at this time. The gonads of all fish except the smaller ones in their first year of life begin to develop in the fall; ovaries contain about 22,000 developing eggs. The maturing pinfish school and leave the estuary in the fall. Food of the remaining fish includes fewer plants, and the amount of food in their stomachs decreases. Usually pinfish form the first annulus on their scales in April of their second year of life.

The life history of Atlantic croakers from this area is similar to that of pinfish. Croakers spawn in the Gulf of Mexico in the late fall and winter,

TABLE 7.—*Atlantic croakers caught per 30-minute trawl-haul in the upper Pensacola Estuary at stations III and IV, 1963–65*[1]

Date	Station III			Station IV			Average both stations
	Average	Confidence interval 95%	Range	Average	Confidence interval 95%	Range	
1963	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
August 22–29	107	63–150	25–229	22	18– 27	11– 34	64
October 21–24	3	2– 5	0– 8	2	1– 2	1– 2	2
1964							
January 6–14	[2]0	[2]0– 0	0– 1	[2]0	[2]0– 0	0– 1	[2]0
February 24–27	0			5	0– 10	0– 16	2
May 5–11	280	218–342	202–463	9	7– 12	5– 16	144
June 22–25	228	81–375	11–527	62	37– 87	19–100	145
July 27–30	74	54– 94	27–110	13	9– 21	5– 26	44
August 24–27	48	21– 74	1–134	41	28– 54	13– 74	44
September 21–24	11	3– 18	1– 26	2	1– 4	0– 7	6
October 26–29	0			0			0
December 8–10	0			11	1– 22	0– 38	8
1965							
January 5–7	1	0– 5	0– 3	22	8– 36	3– 66	17
January 26–28	1	0– 1	0– 1	28	6– 50	0– 77	20
February 23–March 2	2	0– 4	1– 3	15	0– 33	0– 83	12
March 22–31	6	3– 8	2– 14	6	1– 12	0– 26	6
May 3–7	85	43–127	3–172	174	128–220	89–320	130
May 25–28	102	80–124	67–172	495	349–642	135–801	298
June 21–24	221	145–297	67–436	332	284–380	239–408	276
July 26–30	93	17–170	1–378	149	87–212	76–353	121
August 24–27	27	18– 36	10– 47	50	35– 65	17– 85	38
September 20–21	4	0– 8	0– 8	0			2
December 1–3	0			3	0– 10	0– 13	2

[1] 10 trawl-hauls were made at each station per month with the following exceptions (number of hauls in parentheses): Station III, 1964—Dec. 8–10 (3); 1965—Jan. 6 (3), Jan. 28 (4), Mar. 2 (3), Sept. 21 (5), and Dec. 2 (2); Station IV, 1965—Sept. 20 (5), and Dec. 1–2 (5).

[2] Less than 0.5.

and the young move rapidly to the upper estuary; adults rarely reenter the estuary. The young arrive earlier and are more abundant in the winter of years of high water temperatures in November and December but maximum abundance, reached in May or June, seems to be unrelated to water temperatures. The volume of food in the stomachs of croakers is greatest during the first few months after their arrival in the upper estuary. While in the estuary they feed primarily on animals; polychaetes are the dominant food of all sizes of fish. Mollusks, large crustaceans, and fish are eaten in greater amounts as croakers become larger. As croakers grow, the larger individuals move down the estuary causing a stratification by size along the salinity gradient. Migration to the Gulf and gonadal development begin in the late summer and fall. Ovaries of fish in their first year of life contain about 40,000 eggs.

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CONDITIONS RELATED TO UPWELLING WHICH DETERMINE DISTRIBUTION OF TROPICAL TUNAS OFF WESTERN BAJA CALIFORNIA[1,2]

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ABSTRACT

Six oceanographic cruises were made off the west coast of southern Baja California in June through November, 1959–66, and some of the results were compared with contemporaneous fishery data on the distribution of yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Euthynnus pelamis*. The object was to test the hypothesis that the tunas generally do not aggregate in waters cooler than 20° C. even when suitable food is abundant, but do aggregate in warmer waters provided that suitable food is abundant. The measure of abundance of suitable food was the concentration of the pelagic red crab *Pleuroncodes planipes*, a herbivore which is the principal component of the tunas' diet in the Baja California region.

The results supported the hypothesis very well except on the cruise made in June. Then the coastal upwelling was still strong and some tuna entered waters as cold as 17° C., but no colder, where red crabs were abundant. Areas with temperatures 20° C. or over were very limited, and food was generally scarce in them, although it was plentiful in the extensive areas of upwelled water under 17° C. On each of the other five cruises, which covered the period of decay and disappearance of upwelling, extensive areas contained abundant food at temperatures at and over 20° C. Tunas aggregated in or very near those areas, and nowhere else in the cruise region. Red crabs were most abundant in places where their food, phytoplankton (measured as surface chlorophyll *a*), was most plentiful, and in the upwelling season these places were areas of cool upwelled water. The tunas aggregated at first around the edges of the cool areas, which were rich in chlorophyll *a* and red crabs. Later, when surface temperatures in the cores of the cool areas rose past 20° C., the tunas aggregated there as well. Eventually, after all upwelling had ceased, the distribution of surface chlorophyll *a*, red crabs, and tunas became rather uniform off the Baja California coast.

These relations are considered to support the following general statement of tuna ecology, for which there was some prior justification: temperatures set limits of total range, sometimes differently for different species, and food supply determines distribution within the range limits.

Tuna avoid the Cape San Lucas front when it contains water below 20° C., but otherwise the front may have no effect upon them. There is no evidence of aggregation of tuna prey in the front.

As a result of the association of red crabs with phytoplankton (surface chlorophyll *a*) tuna generally occur in the parts of the Baja California region where surface chlorophyll *a* concentrations are relatively high, provided that surface temperatures are not below 20° C. If the region could be thoroughly and frequently monitored for surface temperature and surface chlorophyll *a* during a tuna season, areas of probable tuna aggregation could be specified. It may eventually be practicable to do the monitoring from ships, aircraft, or satellites. It would not suffice to monitor surface temperature only.

Most species of tunas have a wide range in the world's oceans. Their distribution appears to depend mainly upon two oceanic properties: temperature, which sets limits of total range for each species; and standing stock of animals that tuna will eat, which determines distribution within the range limits. This opinion is reasonable, widely held, and supported by a large amount of information (Blackburn, 1965).

Much of the evidence for the hypothesis, however, is indirect. Because tunas are difficult subjects for experiments, tuna ecology depends upon

[1] Contribution from the Scripps Institution of Oceanography, University of California, San Diego, Calif. 92037.

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comparisons between occurrences of tuna and distributions of properties as observed in the ocean. Many of these comparisons have been based on noncontemporaneous data. Distributions of tuna prey have been inferred from other property distributions more often than they have been observed. Different kinds of data on tuna occurrence, some of better quality than others, have been used. The tendency has existed to compare tuna data with environmental data on broad scales of space and time, a procedure which is more suitable for generating hypotheses than for testing them.

The hypothesis must survive tests of detailed close comparison between tuna and environment on narrow scales of space and time if it is to be accepted, but very few suitable tests have been made. The need for a good test became particularly evident about 5 years ago, when plans were being made for a series of oceanographic surveys of the eastern tropical Pacific Ocean (the EASTROPAC Expedition, 1967–68). One of the purposes of the expedition was to identify areas, outside the limits of existing fisheries, in which skipjack tuna, *Euthynnus pelamis*, might be abundant. It was necessary to know whether that purpose would be served by measuring standing stock of tuna prey routinely on the expedition.

The STOR (Scripps Tuna Oceanography Research) Program made a series of cruises off the west coast of southern Baja California to test the hypothesis. This paper gives the results of the test. The area off southern Baja California was selected for the following reasons:

1. It is the area closest to the Scripps Institution of Oceanography in which both yellowfin tuna, *Thunnus albacares*, and skipjack tuna occur regularly in abundance. These are the principal species taken in American tuna fisheries in the eastern tropical Pacific. The most detailed previous study of tuna ecology in the eastern tropical Pacific dealt particularly with yellowfin tuna (Blackburn, 1962, 1963), but the need is now pressing for work on skipjack tuna as well.

2. Yellowfin and skipjack tuna move seasonally from the tropics into the area west of Baja California and then back to the tropics. This shift has been shown by tagging experiments (Schaefer, Chatwin, and Broadhead, 1961; Fink, unpublished). The northern range limits of both species are generally in the area or south of it (fig. 1). Property distributions in the area should, therefore, show which properties correspond with range limits and which do not.

3. The food chain of yellowfin and skipjack tuna is shorter and simpler in the Baja California area than elsewhere in the eastern Pacific in ways that were expected to facilitate the study. In the other areas both tuna species consume a great variety of fishes, crustaceans, and cephalopods, most of which are presumably carnivores (Alverson, 1963). Off the west coast of Baja California, however, both tuna species feed mainly on the galatheid crab *Pleuroncodes planipes* (Alverson, 1963), which is a facultative herbivore and sometimes the dominant herbivore in the area (Longhurst, Lorenzen, and Thomas, 1967). *P. planipes*, frequently called red crab, is commonly pelagic, easy to collect in nets from a research ship, and conspicuous (easy to sort) in net catches. It is the principal species of the micronekton—about 80 percent of the total, by volume—in the area west of southern Baja California (Blackburn, 1968). Boyd (1967) recently published a good illustration.

CalCOFI (California Cooperative Oceanic Fisheries Investigations) has provided much oceanographic information about waters west of Baja California, through a program of seasonally repetitive cruises that began in 1949. IATTC (Inter-American Tropical Tuna Commission) has been recording commercial catches of yellowfin and skipjack tunas in the same area and elsewhere since the beginning of 1951. The IATTC tuna data were suitable for the proposed study, but the CalCOFI oceanographic data were not very suitable because they had been obtained for other purposes. The CalCOFI cruises generally covered only about half the area that yellowfin and skipjack occupy off Baja California (see example in fig. 7); they frequently missed the period when the tunas were most widespread in the area; and they seldom provided any information on phytoplankton or on animals eaten by tuna. It was necessary, therefore, to make special cruises for tuna ecology studies. Five such cruises, together with one CalCOFI cruise that was equipped to serve the same purpose, were made. They covered most of the period of the year (in different years) when tropical tunas occur off Baja California.

The hypothesis to be tested was that yellowfin and skipjack tunas generally do not occur in waters of surface temperature below 20° C., even

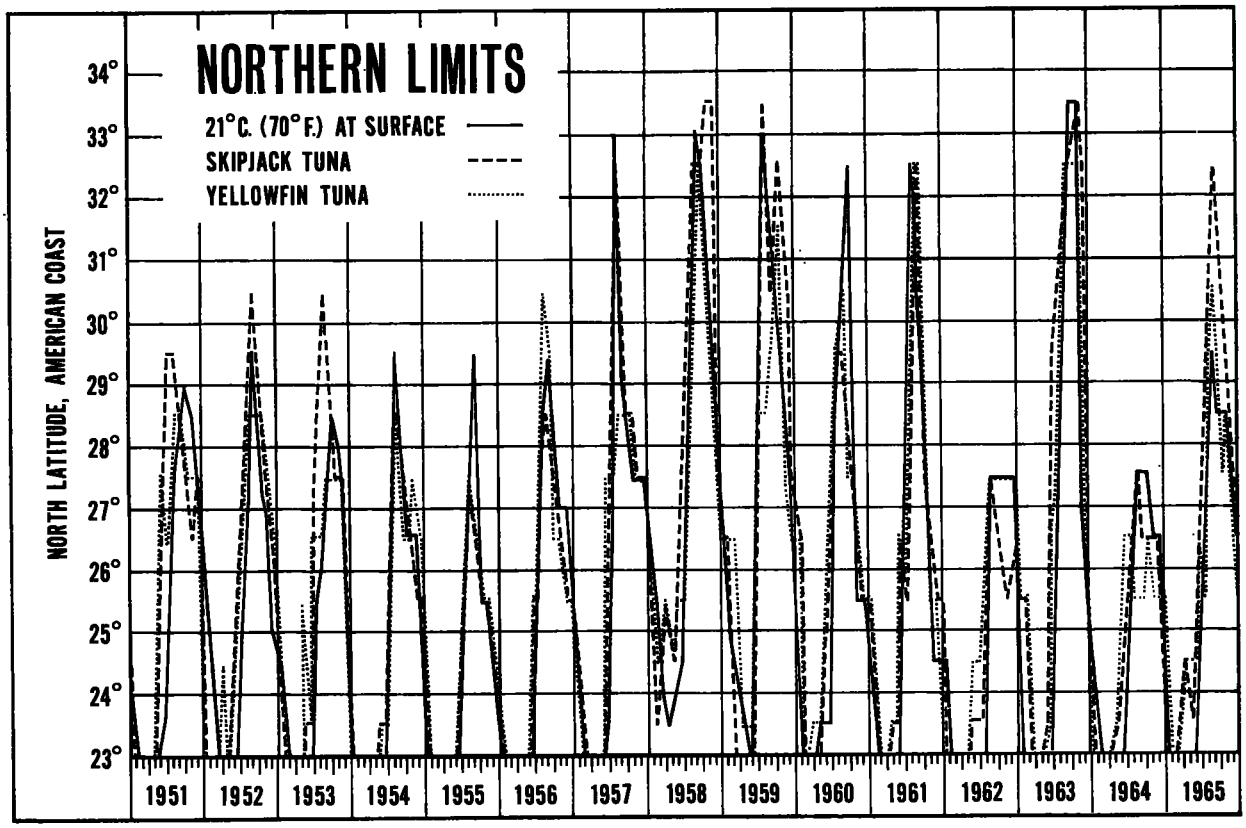

FIGURE 1.—Changes in latitudinal position of the 21° C. surface isotherm and of the northern limits of commercially caught yellowfin and skipjack tunas off the coast of Baja California and California, 1951–65.

when suitable food is abundant in those waters, but do occur in waters of surface temperature at and above 20° C., provided suitable food is abundant. "Suitable food" was defined as pelagic red crab, and "abundant" was defined as a concentration at or above 40 ml. displacement volume per 1,000 m.^{3} of water. The specified temperature, prey species, and concentration of prey are explained below.

The cruises were intended also to identify environmental properties that determine the distribution of the red crab, which is important in the diet of other commercial fishes as well as yellowfin and skipjack tunas (Boyd, 1967). Nothing was known about these properties except that temperature was not one of them (Longhurst, 1967). I thought that the properties would include standing stock of phytoplankton or of zooplankton, depending upon whether the red crab was predominantly herbivorous or carnivorous in the area studied; in the outcome it proved, as expected, to be predominantly herbivorous (Longhurst et al., 1967). Further, the cruises were intended to investigate possible relations between the tuna-connected properties—temperature, prey, food of the prey—and physical features of the environment such as upwellings and fronts. The results of those studies are included in this paper.

The range-limiting temperature was specified in the hypothesis as 20° C. for both species of tuna, but some deviation from it was expected. Range-limiting temperatures for yellowfin and skipjack have been discussed by Uda (1957), Blackburn and associates (1962), Laevastu and Rosa (1963), Broadhead and Barrett (1964), Blackburn (1965), and others. It is evident from these papers that successful commercial fishing, which requires a fairly high concentration of the fish, seldom occurs at temperatures below 20° C. for yellowfin tuna or below 19° C. for skipjack tuna. Both species can occur in waters as cool as 15° C. in some parts of the world, however. In the eastern Pacific the limiting temperature appears to be nearly always close to 20° C. for commercial concentrations of both species. Blackburn and associates (1962)

found that the northern range limits of the species agreed in position with the 21° C. (70° F.) surface isotherm at almost any time. Broadhead and Barrett (1964) showed a similar agreement of both northern and southern range limits with the 20° C. (68° F.) surface isotherm.

Figure 1 shows the kind of data that Blackburn and associates (1962) presented for the period 1951–59, together with similar data for 1960–65. It gives the approximate latitudinal position, in each month of 1951–65, of the northern limit of commercially caught yellowfin tuna, the northern limit of commercially caught skipjack tuna, and the 21° C. surface isotherm. The latitudes shown are those along the entire west coast of Baja California and the southern part of the coast of California. Tuna range limits are based on IATTC catch data that are grouped by 1° squares. They have been graphed at the midpoint of the 1° range of latitude at which the most northern commercial catch (regardless of its amount) was made during the month. Temperatures for 1951–59 are from the series of monthly temperature charts published by Eber, Saur, and Sette (1968), except for August 1952 when CalCOFI cruise data showed a more northward penetration of the 21° C. isotherm. Temperatures for 1960–65 are from monthly temperature charts published by the BCF (Bureau of Commercial Fisheries) Biological Laboratory, San Diego, Calif. Because the BCF temperature data were contoured in intervals of 5° F., including 70° F. (21° C.), it was more convenient to compare tuna limits with 21° C. than with 20° C.

As mentioned previously, figure 1 illustrates the seasonal movement of yellowfin and skipjack tunas along the west coast of Baja California (and in some years, California). It is not a spawning migration for either species (Orange, 1961; Klawe, 1963). The tunas appear west of the southern tip of Baja California (lat. 23° N.) in late spring or early summer, extend their ranges northward during the summer, contract their ranges southward during the autumn and early winter, and leave the area (except in 1958) during the late winter and early spring. The 21° C. surface isotherm changes position in the same way. The positions of the isotherm and the range limits vary from year to year in the same month, but they generally agree closely with one another in any particular month. It is because of this agreement that I think temperature determines the range limits. Figure 1 shows a few disagreements which could have resulted from temperature data or tuna data that were unrepresentative of conditions within a month. The two kinds of data were not collected together. All temperature data apply to the sea surface or the upper 10 m., where yellowfin and skipjack tunas are generally seen and caught.

The range of skipjack tuna appears to be limited also by a high temperature, about 28° C., and the same temperature or a higher one may possibly limit the range of yellowfin tuna (Blackburn, 1965, and references there). Such temperatures seldom occur in extensive areas off western Baja California, however.

Nothing indicates that temperature plays any direct part in determining the patchy distribution of the tunas within their range limits (Blackburn, 1965). According to the hypothesis being tested, food supply is responsible for this aspect of the distribution. The principal food organism of tropical tunas off western Baja California is red crab, as mentioned above. Alverson (1963) sorted stomach contents of 567 yellowfin and 151 skipjack tunas taken off the west coast of Baja California and the coast of California. The composition of the stomach contents of yellowfin tuna by volume was 78 percent red crab, 10 percent northern anchovy, *Engraulis mordax*, and 12 percent other animals (euphausiids absent). The composition of the skipjack tuna stomach contents was 37 percent red crab, 28 percent northern anchovy, 19 percent euphausiids, and 16 percent other animals. Northern anchovies are much more abundant off California and northern Baja California than off southern Baja California, however (Baxter, 1967; Ahlstrom, 1967); in the latter area red crabs are, therefore, probably a larger component of the tunas' diets than Alverson showed. Northern anchovies were very seldom taken on the cruises described in this paper, probably because they were not common in the area. Euphausiids were taken on these cruises, but it was decided not to attempt to study their distribution in relation to that of the tunas, for the following reasons. Euphausiids are more difficult to sort and measure volumetrically than red crabs are; they are not routinely catchable or observable by some of the methods

TABLE 1.—*Concentrations of* Pleuroncodes planipes, *adults and juveniles (not larvae), in ml./10³m.³ of water strained, on cruise TO–64–1*

[Letters under kind of observation signify: M, micronekton haul; Z, zooplankton haul; S, seen in the water. Where concentrations were measured or estimated by more than one method, the highest concentration, corresponding to the first letter, is listed]

Station No.	Kind of observation	Concentration	Station No.	Kind of observation	Concentration	Station No.	Kind of observation	Concentration
		Ml./10³m.³			*Ml./10³m.³*			*Ml./10³m.³*
3	M	32	24	Z	7	53	Z	865
4	Z	69	26	Z	62	54	Z	310
5	Z	34	27	Z	7	55	Z	35
7	Z	7	28	Z	18	56	Z	2,364
9	S	>40	29	M	7	57	Z	1,092
10	M,Z	>40	30	Z	26	58	Z	1,446
11	Z	17	34	Z,M	68	59	Z	614
12	Z	123	35	Z	6	60	Z	225
15	Z	7	36	Z	176	61	Z	108
16	M,Z	72	48	M	46	62	Z	492
17	Z	386	49	Z	5	63	Z	284
18	Z	316	50	Z	43	64	Z	1,142
19	Z	13	51	Z	6	65	Z	80
23	M,Z	36	52	Z	198	66	Z	3,437

that were useful with red crabs (high-speed net catches, and observations at the sea surface); and yellowfin tuna do not eat them. In any event, northern anchovies and some euphausiids are facultatively herbivorous like red crabs and might be expected to have a similar distribution.

I decided to distinguish between concentrations of red crabs that were greater or less than 40 ml./1,000 m.³, as mentioned above. Concentrations above zero ranged from 0.1 to 5,238 ml./1,000 m.³ (tables 1–6), with median 36 ml./1,000 m.³ It is implicit in the hypothesis being tested that tunas, which are highly mobile, encounter and aggregate around the highest concentrations of food in any area which they enter. It was, therefore, desirable, on the one hand, to use some value at least as high as the median to distinguish high concentrations from low. On the other hand, the frequencies at successive intervals of concentration declined sharply above the median, to the extent that charting would have been difficult if a value appreciably over 100 ml./1,000 m.³ had been used. Trial made it evident that the property charts presented later, and the conclusions of the study, were much the same at a value of 40 (just above the median) and at 100 ml./1,000 m.³ Therefore, the former value, which made more data available for drawing isograms of abundance of red crabs on the charts, was chosen.

MATERIAL AND METHODS

The following sections give information about the cruises and stations from which data were obtained; the methods used for measuring surface temperature, surface chlorophyll *a*, and concentration of red crabs; and the kinds and sources of contemporaneous data on tunas.

CRUISES AND STATIONS

The oceanographic data for this study were obtained in six cruises—one made in 1959, which generated the hypothesis mentioned above, and five made in 1964–66. The area of study was restricted to south of lat. 28° N., where the tunas (fig. 1) and red crabs (Longhurst, 1967) occur each year; these species appear farther north in some years, but not in all. Figure 2 identifies localities and topographic features to which I refer in this paper. The principal banks (underwater elevations of the bottom) within and beyond the 100-fathom (183-m.) line, and the small islands known as Alijos Rocks, are shown. Tuna fishermen consider that these features represent good fishing areas, a matter which is discussed later.

The tracks and station positions for the six cruises are shown in figures 3, 5, 7, 9, 11, and 13, which appear in later sections of this report. They were based on the CalCOFI basic station plan (since 1950), and most of the stations can be identified easily with CalCOFI station positions (Anonymous, 1963), although they have not been numbered in the CalCOFI way. Two of the cruises were devoted entirely to occupying a series of CalCOFI stations (figs. 7 and 9). On each of the other four cruises (figs. 3, 5, 11, and 13) a series of CalCOFI stations was occupied first (part 1 of the cruise, terminating in the southern part of the area) and the ship then returned northward by a different route, occupying special stations in areas of particular interest (part 2 of the cruise). The

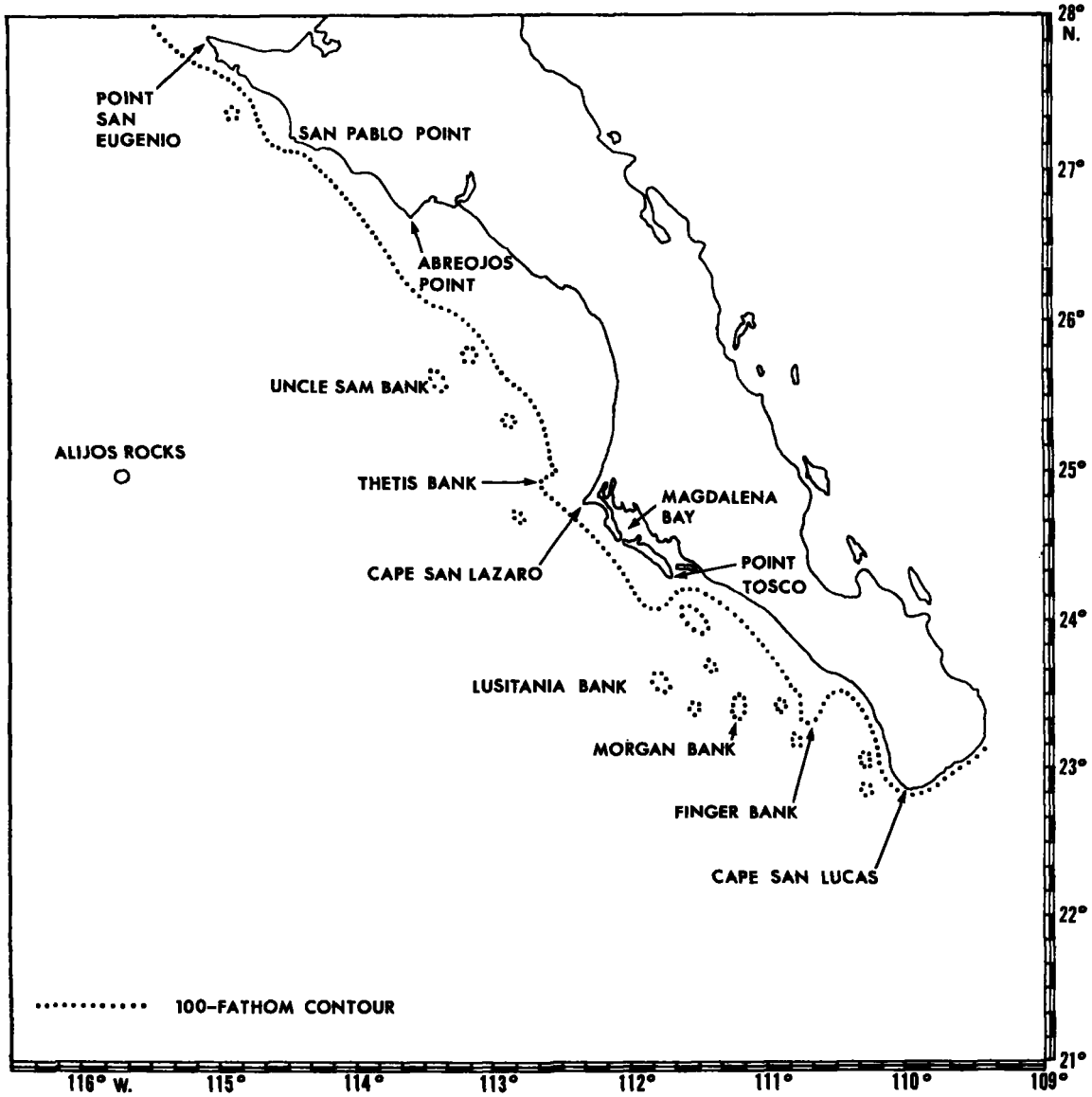

FIGURE 2.—Localities and topographic features referred to in the paper.

figures identify the stations that were occupied close to local noon and midnight so as to indicate approximately which portions of the track were covered in daylight and which in darkness.

Although many physical, chemical, and biological properties were measured at several depths at most stations, this paper is concerned only with data on surface temperature, standing stock of phytoplankton, pelagic crabs, and tunas, for reasons given earlier. The stock of phytoplankton was measured as concentration of chlorophyll *a*, and in this paper I discuss only surface concentrations, which were measured much more often than concentrations at other levels.

SURFACE TEMPERATURE

The term "surface temperature" is used for convenience, for the temperature data in this paper are not precisely from the sea surface. Mainly they are from 10 m. below the surface, where temperature was measured at almost every station with a reversing thermometer. Temperatures read from bucket thermometers, bathythermographs, and thermographs that recorded sea-water injection

temperatures aboard vessels were used in charting isotherms between station positions. The data for cruises TO–59–2 (considered as part of CalCOFI cruise 5908), 6608, TO–64–1, and TO–64–2 have been published (Scripps Institution of Oceanography, 1961, 1968, 1969). The data for cruises TO–65–1 and TO–66–1 are available from the Scripps Institution of Oceanography.

SURFACE CHLOROPHYLL *A*

On cruise TO–59–2, concentrations of chlorophyll *a* were determined by spectrophotometric measurement of optical density of acetone extracts by use of the equations of Richards with Thompson (1952). These data have been published (Blackburn, Griffiths, Holmes, and Thomas, 1962). On cruises TO–64–1 and TO–64–2, concentrations were determined by measuring the fluorescence of acetone extracts (Holm-Hansen, Lorenzen, Holmes, and Strickland, 1965; Lorenzen, 1966). The data have been published (Scripps Institution of Oceanography, 1969). On the other three cruises, determinations were made by measuring the fluorescence of acetone extracts or in vivo suspensions (Lorenzen, 1966) or both. The data for these cruises are available at the Scripps Institution of Oceanography. All available surface measurements were used in this study, irrespective of the time of day or night at which the material was collected. Concentrations are given in mg./m.^{3}

PELAGIC RED CRABS

The pelagic red crab was collected or observed and its concentration in the water estimated in several ways. Tables 1–6 list stations and localities between stations where red crabs were collected or observed on the six cruises and give the estimated concentrations in milliliters (displacement volume) /1,000 m.^{3} These data refer to adults and juveniles (postlarvae), but not larvae.

One method of collection (M in tables 1–6) was the standard micronekton net haul, which was made usually once each night. The net was the 1.5-m. (5-foot) net described by Blackburn (1968); it was hauled obliquely at a ship speed of 5 knots (9.3 km./hour). On cruises TO–59–2, TO–65–1, and TO–66–1, the hauls were made to a depth of about 90 m. with 350 m. of wire. On cruises TO–64–1 and TO–64–2 they were made to about 140 m. with 500 m. of wire. Wire was paid out at speeds of 20 to 30 m./minute and retrieved at speeds of 10 to 15 m./minute. This method was not used on cruise 6608; other methods, mentioned below, were employed on that cruise. The volume of water strained on each haul was estimated from the distance traversed in meters, the mouth area of the net in square meters, and an empirical filtration coefficient, 0.76 (Blackburn, 1968). Crab volumes were measured directly.

Another method (Z in tables 1–6) was the standard zooplankton net haul with the CalCOFI 1-m. net, which was usually made at each station. These hauls were made obliquely to a depth of about 140 m. at a ship speed of less than 2 knots (3.7 km./hour). Thrailkill (1956) described the net and hauling procedure. A flowmeter measured the volume of water strained on each haul. Volumes of red crabs were measured directly for cruises TO–64–1, TO–64–2, and TO–65–1. For the other three cruises the volumes were estimated from counts of crabs, using an empirical average volume of 3.0 ml. per crab, or 1.0 ml. per crab if they were recorded as small. Some crabs probably avoided these slowly moving nets, even at night. At 46 night stations both standard micronekton hauls and standard zooplankton hauls were made and red crabs collected. Volumes per 1,000 m.^{3} were equal in the two hauls at 3 stations, greater in the micronekton hauls at 31 stations (including 18 when the zooplankton haul was negative), and greater in the zooplankton haul at 12 stations (including one with a negative micronekton haul).

A third method (H in tables 1–6) was the high-speed micronekton net haul described by Blackburn (1968). This net is hauled horizontally at about 10 m. below the surface at the ordinary cruising speed of the ship. Such hauls were made, usually at night, on all cruises except TO–64–1. Their duration was from 2 to 3 hours on cruise TO–59–2, from ½ to 1½ hours on cruise TO–64–2, and 1 hour on other cruises. The volume of water strained was estimated from the distance traversed, the mouth area of the net, and an empirical filtration coefficient, 0.94 (Blackburn, 1968). Crab volumes were measured directly. I showed earlier (Blackburn, 1968) and found again in this study that volumes per 1,000 m.^{3} from these hauls average much smaller than those from standard micronekton hauls made at about the same time and place; the ratio, high-speed net volume/standard

micronekton net volume, is of the order 1 : 10. The reasons are unknown; possibly red crabs are scarcer in the upper 10 m. than at greater depths, or they may tend to avoid a fast-moving ship. The concentrations shown for this method in tables 1–6 have all been multiplied by 10 to make them broadly comparable with those from the other hauls.

The remaining sources of information about red crabs were sightings of aggregations at the sea surface and occurrences in the stomachs of predators that were captured from the ship. The concentration for each sighting was obviously over 40 ml./1,000 m.^{3} and is listed accordingly (see S in tables 1–6). On four occasions the stomachs of predators contained crabs. The predators were yellowfin tuna, dolphin, *Coryphaena hippurus*, and an unidentified turtle. Three of these occurrences were represented by only one predator individual; it was not then safe to assume that red crabs occurred at a concentration over 40 ml./1,000 m.^{3} In the other occurrence, three predator individuals (yellowfin tuna) containing red crabs were captured and many others seen; here it was reasonable to assume that a high concentration of red crabs was available (see P in table 5).

For stations at which two or more estimates of concentration were available, the highest one was listed in tables 1–6. In charting the isogram of 40 ml./1,000 m.^{3} concentration for each cruise, I used the data of tables 1–6, together with the zero concentrations recorded for the remaining stations. In view of the opinion of Boyd (1967) and Longhurst (1967) that red crabs make diurnal vertical migrations, I occasionally ignored estimates of low or zero concentrations based upon daytime catches or observations when other evidence suggested the probability of high concentrations in the area—for instance when surface chlorophyll *a* was high, and high concentrations of crabs were encountered during one or both of the adjacent nights. An additional justification for this procedure is that most of the daytime information was obtained from zooplankton hauls, which frequently yield low estimates of concentration as shown above. On the other hand, if a series of night observations all yielded low estimates of concentration I concluded definitely that red crabs were not abundant in the area examined, whatever the other circumstances were; I sometimes ignored an occasional low concentration in a series of high ones obtained during the same night.

Stations 60–66 of cruise TO–64–1 were occupied very close to each other, in an area of about 5 nautical miles (9 km.) radius, during a period of about 3 days. The odd-numbered stations were occupied about noon, the even-numbered stations about midnight. Table 1 shows the crab concentrations measured in zooplankton hauls at these stations which were all much higher than 40 ml./1,000 m.^{3} Concentrations were lower at noon than at midnight, as expected. Concentrations in consecutive hauls differed by a factor of about three in both the noon and midnight series. I have found similar differences for other kinds of organisms in noon and midnight series of micronekton hauls that were closely adjacent in space and time (Blackburn, 1968). Concentrations of red crabs estimated from single net hauls might, therefore, differ by a factor up to three from concentrations actually present in the water. I tried to allow for this possibility in charting the isogram of 40 ml./1,000 m.^{3} for each cruise.

TUNAS

Data on the recorded occurrence of yellowfin and skipjack tunas were obtained from IATTC, which has such data in various forms, one of which gives average catch per unit of fishing effort by species, by fishing method (live-bait and purse-seine), location by 1° squares, and by months. Such information had been very useful in previous work on tuna ecology in the Gulf of Tehuantepec (Blackburn, 1963) but was rather unsatisfactory for this study. The isograms of temperature, chlorophyll *a*, and red crabs intersected the parallels and meridians in a way that was frequently very complicated (e.g., fig. 6), and it was evident that their position did not always remain unchanged for the whole of the calendar month in which they were observed.

I used IATTC data on tuna occurrences that had definite dates and positions. Figures 4, 6, 8, 10, 12, and 14 (see later sections) show these occurrences separately for each species and for mixed catches of the two species. They refer either to the whole period when the ship was in the area of the charts or to some part of that period, as explained later for each cruise. The original data were available from baitboats and purse seiners separately, but the distributions of tuna from these two

sources were generally similar and are not distinguished in this paper. Data were available on the amounts of tuna captured at each of the charted positions, but they are not given here because size of catch is not necessarily a measure of abundance. Catch per unit of fishing effort can be considered as a measure of abundance, but it would be difficult to establish the amount of effort expended at each of the individual points shown on the charts. For this study, any commercial catch of tuna indicates an aggregation of the fish, and the main interest lies in the general distribution of the aggregations.

In areas where no occurrences are shown, there was either no significant fishing effort (hence tuna distribution unknown) or no fish, at the period of the cruise. Data showing absence of fish are few; they refer to combinations of 1° squares and months in which at least 5 boat-days of fishing effort yielded no catches. These examples of unproductive effort are mentioned later for the individual cruises.

A few catches and observations of yellowfin and skipjack tunas made from the oceanographic vessels have been included in the charts.

RESULTS OF INDIVIDUAL CRUISES

In the following sections, six cruises are discussed in the order that best represents the typical seasonal change during the period of the year when yellowfin and skipjack tunas occur west of Baja California. The distributions of surface temperature, surface chlorophyll *a*, red crabs, and tunas are described and explained for each cruise, with special reference to their relations with the seasonal cycle of coastal upwelling.

CRUISE TO–64–1

This cruise showed environmental conditions that are probably typical of the beginning of a yellowfin and skipjack tuna season off western Baja California (see fig. 1). Figure 3 shows the track and station positions, omitting individual positions of two clusters of stations that were occupied for special purposes. Figure 4 gives the essential features of the distributions of the properties previously discussed; this and similar figures show only selected isograms of surface temperature and surface chlorophyll *a*. The isotherms in figure 4 refer only to the temperature distribution on part 1 of the cruise, June 9–15, 1964. At the few stations that were re-occupied on part 2 of the cruise, temperatures averaged about 2° C. higher than on part 1. Figure 4 includes only those tuna occurrences that were recorded for the period June 9–15. The charted distributions of chlorophyll *a* and red crabs are based on all available data from the entire cruise, as they are also for the other cruises. The red crab data are given in table 1.

Along the Baja California coast below Point San Eugenio the coastal upwelling typically begins about April, is strong from April through June, and ceases about August (Reid, Roden, and Wyllie, 1958; Wyllie, 1961; Lynn, 1967). CalCOFI stations 123.37 and 143.26, which are the same as stations 2 and 18 in figure 3, are considered to be the centers of the two principal coastal upwelling areas (Lynn, 1967). These areas, one along the coast south of Point San Eugenio and the other south of Cape San Lazaro, are indicated by the 15° C. surface isotherm in figure 4. In the northern area, surface temperatures below 13° C. were recorded off San Pablo Point. The 16°, 17°, and 18° C. isotherms lie generally parallel to the coast, rather than in the wavy configurations described later for certain offshore isotherms on subsequent cruises. This parallel orientation appears to be normal in June (Anonymous, 1963).

Off Cape San Lucas a well-defined temperature front existed at the sea surface, oriented in much the same way as in May 1960 and April 1961 (Griffiths, 1963, 1965). Surface water below 17° C., in part below 16° C., lay in a narrow band just west of Cape San Lucas; it was probably upwelled farther north, where temperatures were similar. Eastward from this cold area along the south coast of the peninsula, surface temperatures rose to above 25° C. The 17° to 21° C. isotherms trended more or less to the southeast from Cape San Lucas, whereas the 22° to 25° C. isotherms trended parallel to the south coast of Baja California. The front, therefore, was very strong close to Cape San Lucas but split about 15 nautical miles (28 km.) offshore into two weaker parts. Some 60 miles (110 km.) southwest of Cape San Lucas, a tongue of water over 19° C., mostly over 20° C. (the two isotherms are close together), protruded north-

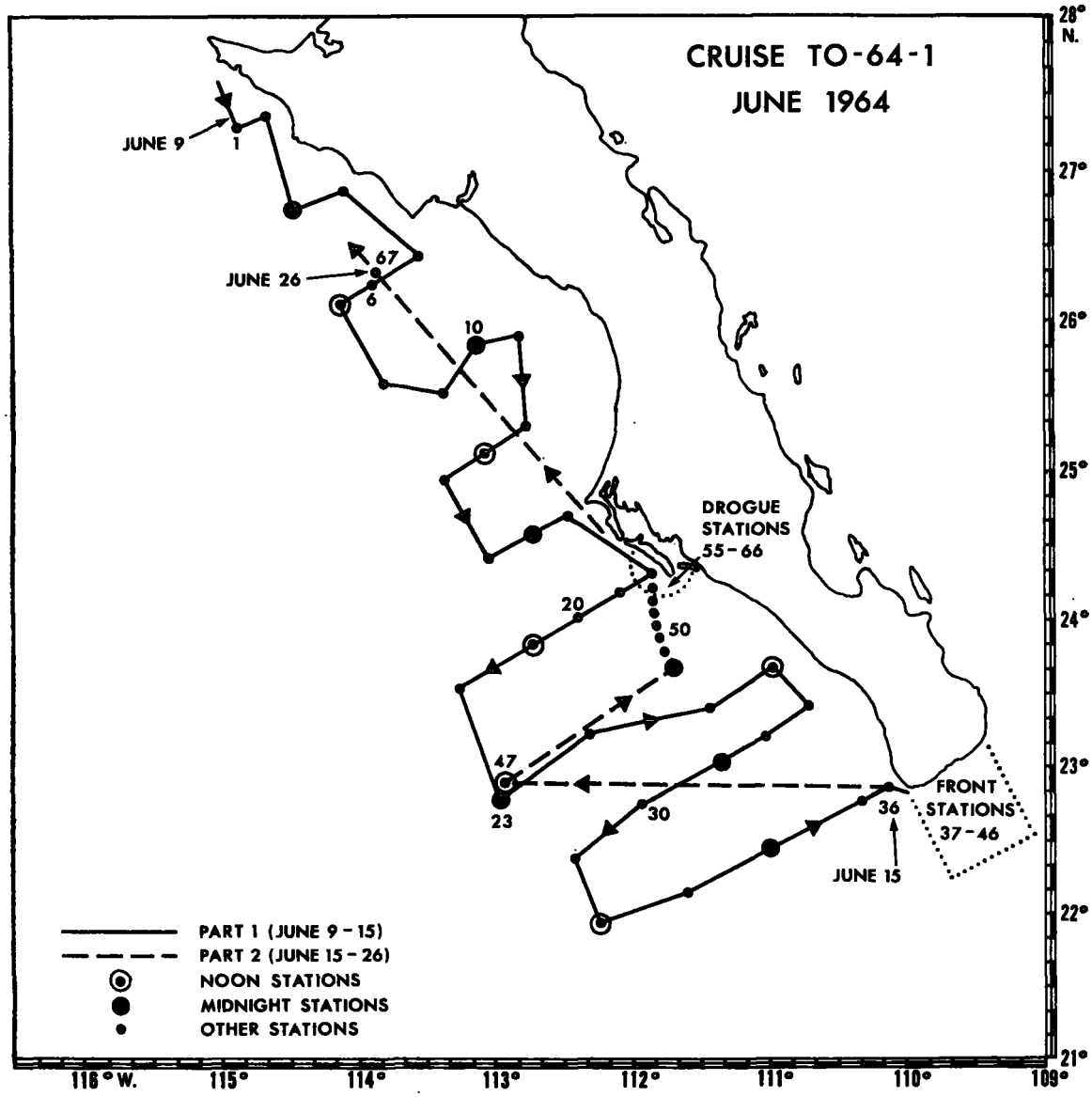

FIGURE 3.—Track and station positions for cruise TO-64-1.

ward into the cruise area. Such a warm tongue appears frequently at this time of year; for example, it occurred in June 1951 and June 1957 (Anonymous, 1963) and is shown in several of the BCF June temperature charts.

The standing stock of surface chlorophyll *a* was highest in the cold coastal water (upwelling or recently upwelled water), as expected. The 1.0 mg./m.^{3} isogram follows the coast and includes the principal upwelling areas, where some concentrations exceeded 6.0. Concentrations below 0.1 mg./m.^{3} were confined to the offshore region in the extreme south of the area (stations 31–34), and none of these values was below 0.06.

The area of red crab concentration over 40 ml./1,000 m.^{3} was large and broadly similar to that of chlorophyll *a* concentration over 1.0 mg./m.^{3} Thus, the red crab and its food supply had the same distribution. A separate small area of high concentration lay near Cape San Lucas, and another one farther offshore.

The tuna occurrences were in two groups in the southern part of the area—one (yellowfin tuna only) east of the front along the south coast of

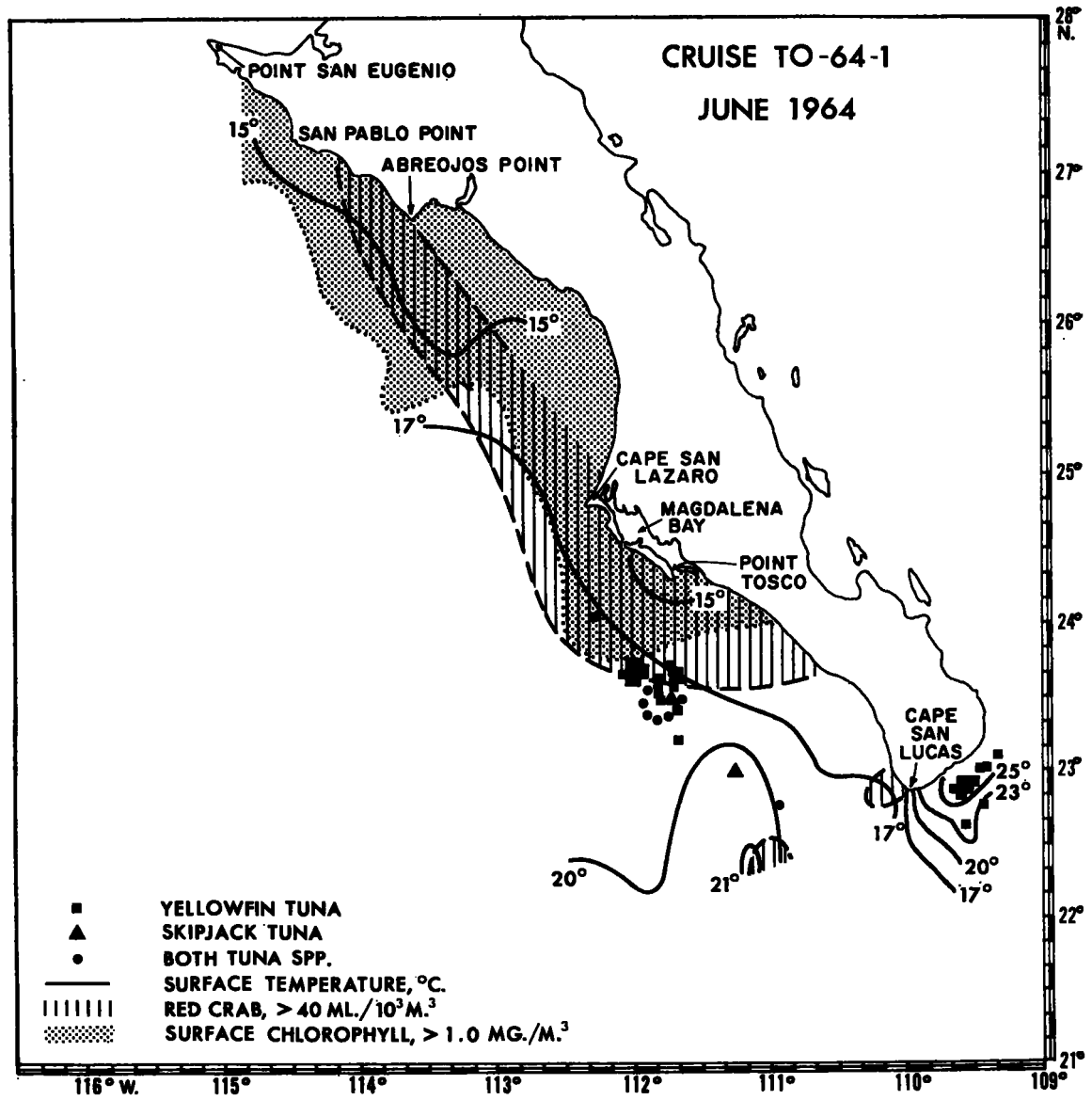

FIGURE 4.—Distributions of surface temperature, surface chlorophyll *a*, and red crabs for cruise TO-64-1 and locations of contemporaneous tuna catches.

Baja California, and the other (both species) in and northwestward of the warm offshore tongue. Neither of these groups of tuna was in the area of highest concentration of food, although the second group reached the edge of it. In the front area virtually no red crabs were caught in three standard night micronekton hauls, and concentrations of all animals in these hauls (i.e., all potential tuna prey) ranged only from 9 to 16 ml./1,000 m.³ In the other tuna area concentrations of red crabs were 7 and 46 ml./1,000 m.³ at stations 29 and 48, and concentrations of all other micronekton were 14 and 10 ml./1,000 m.³ Some of the tuna aggregations in each of these areas were only about 25 nautical miles (46 km.) from a much richer food supply (over 100 ml./1,000 m.³ of red crabs—e.g., at station 52), but the fish would have had to encounter temperatures below 17° C. to reach it. Figure 4 shows that the tunas will tolerate 17° C. and suggests that lower temperatures are not acceptable.

A reasonable interpretation of figure 4 is that

both tuna species prefer some temperature at or over 20° C., will move into adjacent water as cool as 17° C. if food is more plentiful there, and will not enter water below 17° C. even if food is extremely abundant. If so, tuna will not round Cape San Lucas from the east as long as water under 17° C., and perhaps under 20° C., remains there; data from Griffiths (1963) indicated that 20° C. was the limiting temperature in May 1960. Under those circumstances their entry into the area west of Baja California will be by the offshore tongue of warm water, as suggested by figure 4. The area enclosed by the offshore 20° C. isotherm in figure 4 was well occupied by both species in the second half of June and the first half of July, although there were still no records of tuna caught between that area and the coast (between long. 110° and 111° W.). Tuna were not recorded in the latter area until the second half of July, when they suddenly became widespread; these fish were all yellowfin tuna, and probably the same aggregations as shown to the east of the front in figure 4. Probably the 20° C. isotherm moved northward from Cape San Lucas about mid-July and permitted the yellowfin tuna to round Cape San Lucas; this isotherm was located at about lat. 25° N. during the last 10 days of July (Scripps Institution of Oceanography, 1966). Thus, tuna appear to follow two pathways from the tropics into the area west of Baja California at the beginning of a tuna season, both determined by the distribution of surface temperature. One is from the east around Cape San Lucas, and the other is from the south. The former is mainly for yellowfin tuna, and the latter is for both species; skipjack tuna are much less common than yellowfin tuna to the east of the meridian of Cape San Lucas in most years (Joseph and Calkins, 1969).

Cruise TO–64–1 was the only one of this series in which tuna occurred at temperatures substantially lower than 20° C. They probably can tolerate temperatures down to 17° C. to obtain a larger food supply, as indicated above. Lee (1952) found that cod will enter waters over 2° colder than those in which they usually occur if food is plentiful. On cruise TO–64–1 only one small area had more than 40 ml./1,000 m.^{3} of red crabs in water at 20° C. or over (station 34, with 68 ml./1,000 m.^{3}). On all the later cruises, such areas were extensive and the concentrations of red crabs in them were generally over 100 ml./1,000 m.^{3}

Several tuna boats were fishing off the south coast of Baja California at the time the front was surveyed, and their operations were watched to see if their fishing success bore any relation to the position of the front. The only obvious relation was that they worked mainly to the east or north of the front and occasionally on its warm edge. They were probably avoiding water under about 20° C., and the front itself, as distinct from the limiting isotherms located in it, seemed to have no effect.

Various authors have suggested that tunas may aggregate in fronts in response to aggregations of prey organisms. Griffiths (1963, 1965) found that some kinds of zooplankton were more abundant in the middle of the Cape San Lucas front than on either side of it, but, on the other hand, micronekton (potential tuna forage) was most abundant on the warm side. On cruise TO–64–1 micronekton hauls were again made on both sides of the front and in the middle, all on the same night; the highest concentration was on the warm side, as in Griffiths' series, but all three concentrations were similar (16.3 ml./1,000 m.^{3} warm side; 9.1, middle; 11.8, cold side).

All the foregoing observations were made in the part of the front that is oriented parallel to the south coast of Baja California. Another series of seven micronekton hauls, made across the stronger part of the front near Cape San Lucas on cruise TO–64–1, showed highest concentrations in the upwelled water on the cold side. The evidence, therefore, does not support the idea of a concentration of tuna forage in the Cape San Lucas front. This front may have no special attraction for tunas and is probably avoided by them when unsuitably cold water occurs in it.

CRUISE TO–64–2

The results of this cruise, which was made in August of a rather cold year (see fig. 1), are probably typical of conditions in the early part of the tuna season, including July, when the fish rapidly expand their range northward. Figures 5 and 6 show cruise coverage and property distributions. The isotherms in figure 6 refer to the temperature distribution on part 1 of the cruise, August 5–16, 1964. At the few stations that were re-

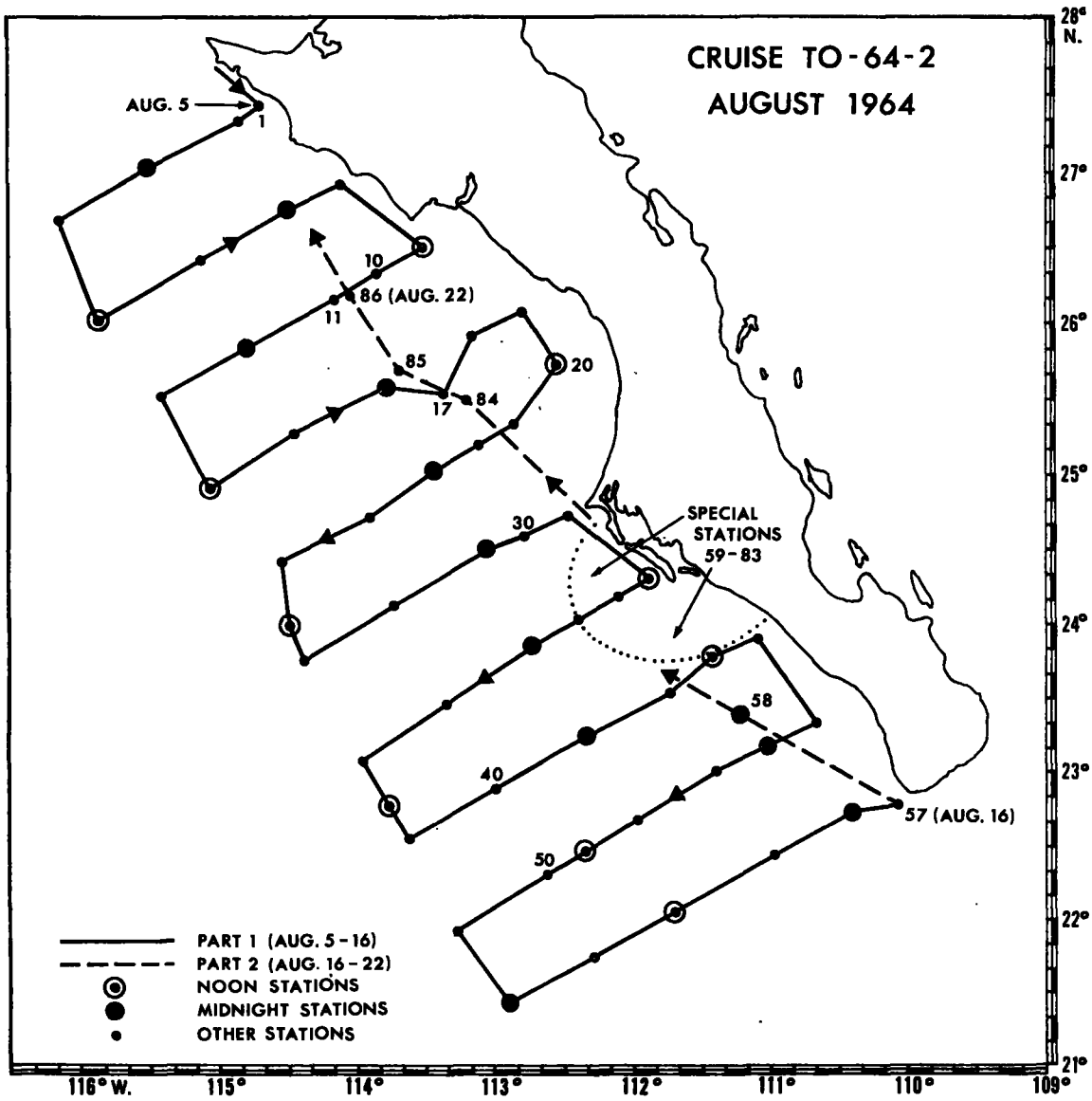

FIGURE 5.—Track and station positions for cruise TO–64–2.

occupied on part 2 of the cruise, temperatures were about the same as on part 1 except on August 21 and 22, when they were about 2° C. higher. Figure 6 includes only those tuna occurrences that were recorded for the period August 5–20. The red crab data are given in table 2.

Detailed surface temperature charts for the area in July and August show in most years a different configuration of isotherms from that found in June (Anonymous, 1963). Instead of lying more or less parallel to the coast, the isotherms become wavy; tongues of relatively cool water extend away from the coast, separated from each other by tongues of relatively warm water extending toward the coast. Figure 6 shows this situation very well; cold tongues run offshore from the two principal upwelling areas identified on cruise TO–64–1, and the northern area gives rise to at least two tongues. This distribution is probably caused by the eddies that characteristically appear about July and August (Wyllie, 1966). In figure 6 and later figures, the isotherms selected for charting always included those which showed the tongues, if present, in most detail. Temperatures under 20° .

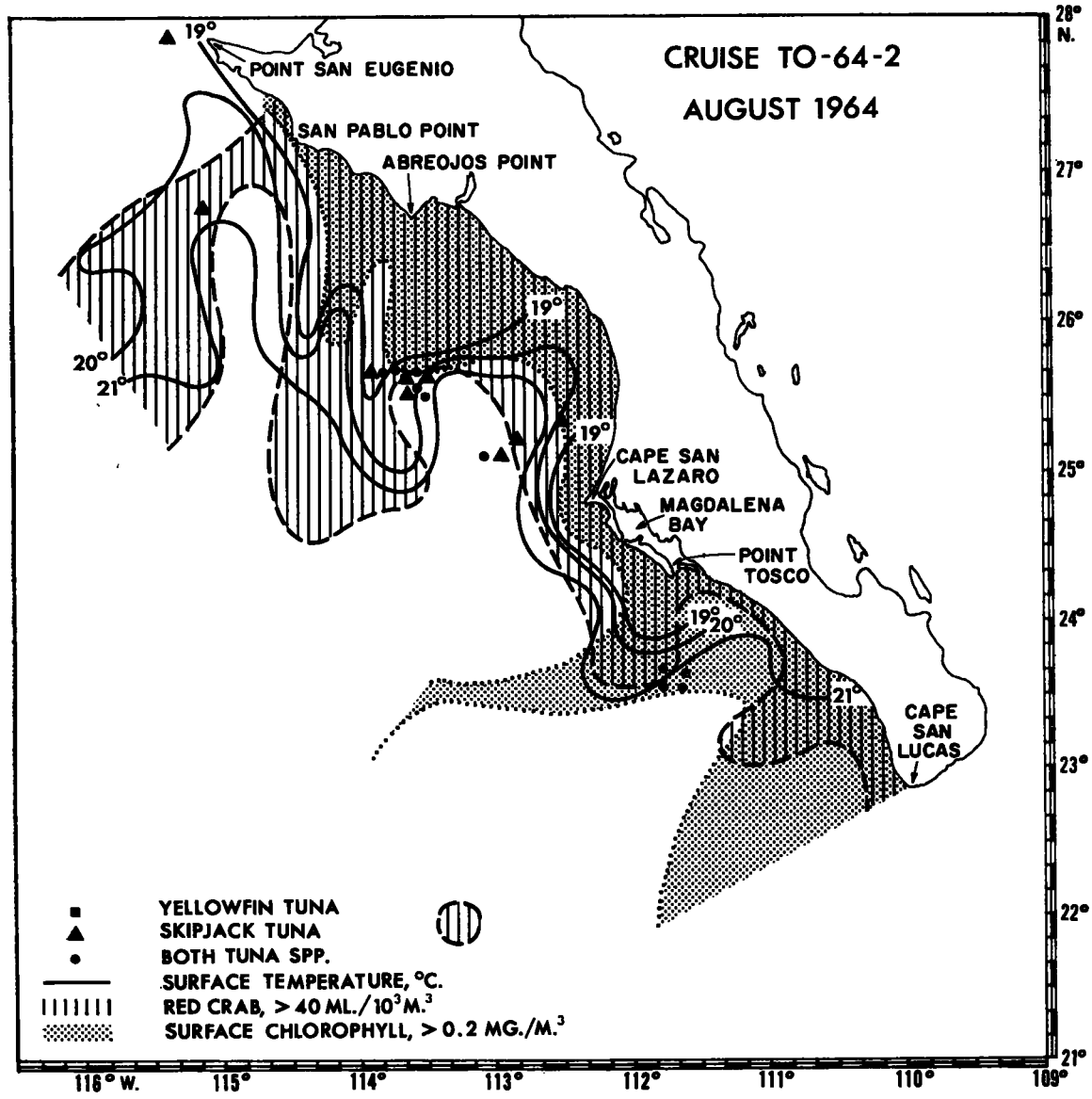

FIGURE 6.—Distributions of surface temperature, surface chlorophyll *a*, and red crabs for cruise TO–64–2 and locations of contemporaneous tuna catches.

occurred almost all along the coast on cruise TO–64–2; minima, at stations 1, 8, and 31, were between 15° and 16° C., and maxima, at stations 53 and 54, were between 26° and 27° C.

Concentrations of surface chlorophyll *a* ranged from 6.4 to 0.01 mg./m.³ Their generally much lower values than on cruise TO–64–1 reflect some decay in the upwelling regime. Only station 32 had a concentration above 1.0 mg./m.³ The isogram of 0.2 mg./m.³ in figure 6 follows rather closely the edge of the cool water, except in the extreme northwestern part of the area covered. It protrudes farther offshore between lat. 23° and 24° N. than the corresponding protrusion of the isotherms. The 0.1 mg./m.³ isogram (not shown) follows it closely in most areas.

The position of the isogram showing 40 ml./1,000 m.³ of red crabs is close to the 21° C. isotherm and the 0.2 isogram of chlorophyll *a*, except in the northwestern part of the area (fig. 6). In general, relatively high standing stocks of red crabs and

TABLE 2.—*Concentrations of* Pleuroncodes planipes, *adults and juveniles (not larvae), in ml./10³m.³ of water strained, on cruise TO–64–2*

[Letters under kind of observation signify: M, micronekton haul; Z, zooplankton haul; H, high-speed net haul between stations; S, seen in the water. Where concentrations were measured or estimated by more than one method, the highest concentration, corresponding to the first letter, is listed]

Station No.	Kind of observation	Concentration	Station No.	Kind of observation	Concentration	Station No.	Kind of observation	Concentration
		Ml./10³ m.³			*Ml./10³ m.³*			*Ml./10³ m.³*
4–5	H	520	30–31	H	143	58–59	H	165
7	Z,M	63	32	Z	531	60	S	>40
7–8	H	>40	34	Z	4	63	Z	108
12	Z,M	24	36	Z	13	64	Z	17
12–13	H	18	40	Z	11	65	Z	33
12–13	H	879	44	Z	9	69	Z	54
13	S	>40	45	S	>40	70	Z	9
16	M	1	46	M,Z	355	73	Z	9
16–17	H	190	50	Z	4	74	Z	7
17–18	H	333	51	Z	48	75	Z	13
17–18	H	18	51–52	H	3	76	Z	89
23	M	7	52	M,Z	37	77	Z	197
23–24	H	268	52–53	H	35	78	Z	26
23–24	H	>40	55	Z	6	79	Z	562
24	Z	11	56	M	1	80	Z	232
24–25	H	314	56–57	H	83	81	Z	101
27	Z	4	57	Z	13	(1)	M	>40
29	M	1	58	Z,M	5			

[1] Series of night surface hauls with the large micronekton net near Uncle Sam Bank.

chlorophyll *a* occurred together in the upwelling or in recently upwelled water.

The occurrences of tuna (both species) were on the edges of the area of high concentration of red crabs where surface temperatures were all between 22° and 18° C. No tuna were recorded in the large inshore areas where red crabs were equally or more abundant and temperatures were lower; the fish probably avoided these areas. One 1° square, bounded by lat. 26° and 27° N. and long. 114° and 115° W., had a significant amount of fishing effort (six boat-days) that yielded no tuna in the month of the cruise. According to figure 6, almost all of this area was either colder than 20° C. or had less than 40 ml./1,000 m.³ of red crabs; it is not surprising then that tuna were not found. Elsewhere, in areas where no occurrences are shown in figure 6, the distribution of yellowfin and skipjack tunas at the time of the cruise is not known. Tunas could have occurred along other parts of the edge of the cool, food-rich, water.

Figure 6 shows an isolated occurrence of abundant red crabs far offshore, where surface chlorophyll *a* was below 0.1 mg./m.³ and tuna distribution unknown. Such offshore distributions, which Boyd (1967) and Longhurst (1967) have reported previously, may represent individuals that the California Current has carried out of the coastal region.

CRUISE 6608

This CalCOFI cruise, made in August 1966, covered only part of the area of interest. The results represent conditions at a slightly later stage in the year than those for cruise TO–64–2. The CalCOFI stations have been given serial numbers as shown in figure 7. Figures 7 and 8 show cruise coverage and distributions of properties. The red crab data are given in table 3.

The surface isotherms (fig. 8), especially 23° C., show the same tonguelike distributions as before. Cool tongues ran offshore from areas which lie south of Point San Eugenio and Abreojos Point; here a small inshore belt of upwelling or upwelled water under 20° C. occurred. Warmer water lay on both sides of these tongues. Surface temperatures for the whole area were between 17° and 26° C.—very close to the range (16°–25° C.) in an average August (Anonymous, 1963).

Concentrations of surface chlorophyll *a* ranged from 2.0 to 0.03 mg./m.³, but those over 1.0 mg./m.³ were confined to a small inshore area between Point San Eugenio and San Pablo Point. It was not possible to draw an isogram for 0.1 mg./m.³ with confidence, because observations were not made in some parts of the area. In general, concentrations below 0.1 mg./m.³ were in water over 23° C., outside the main cool tongue shown in figure 8, but some of them were in the small (eastern) cool tongue as well. All concentrations above 0.2 were in the cooler water, as expected. They are charted in figure 8 to show two areas, which may, however, have been joined, because observations were not made between them.

The sampling of red crabs on this cruise was

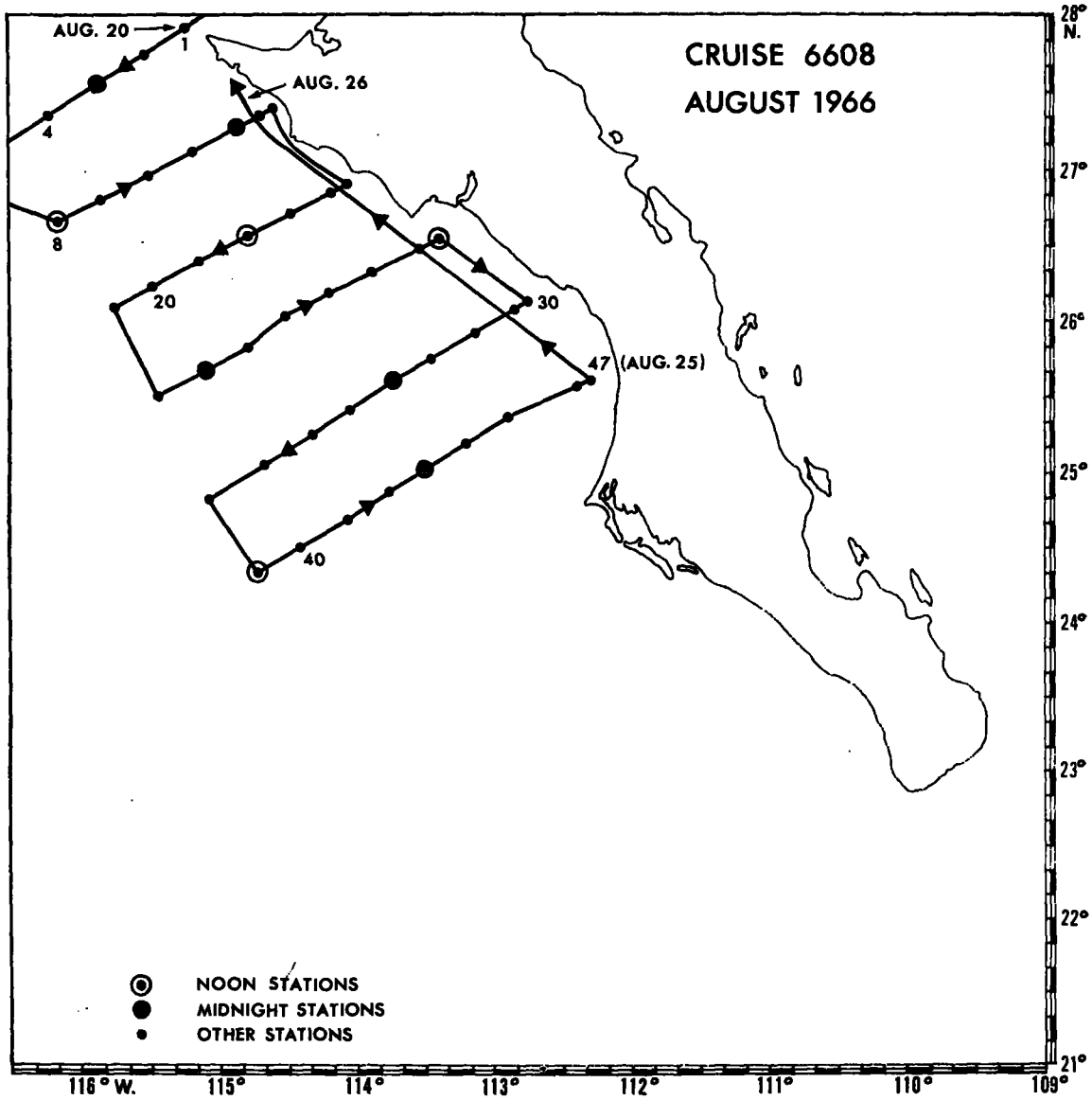

FIGURE 7.—Track and station positions for cruise 6608.

more restricted than on most of the other cruises because no standard micronekton hauls were made. Figure 8 shows four areas with concentrations over 40 ml./1,000 m.^{3} The northern area was in water which was cool and rich in chlorophyll *a* (over 0.2 mg./m.^{3}); the eastern area was partly in and partly adjacent to the same kind of water; the southwestern area was in and adjacent to a tongue of cool water, with chlorophyll *a* concentrations about 0.1 mg./m.^{3}; and the remaining small area was in warmer water where no chlorophyll data were obtained.

The data on tuna occurrence for the period of the cruise, August 20–26 (fig. 8) show a single record in the northern part of the area, located, like those on cruise TO–64–2, on the edge of an area that was rich in food but rather cold. The other records show a distribution of tuna right across one of the tongues of cool water, where temperatures were nevertheless high enough (over 20° C.) to permit the tuna to exploit the high concentration of red crabs; the tuna were located partly in and partly on the edge of this concentration of food. A significant amount of fishing

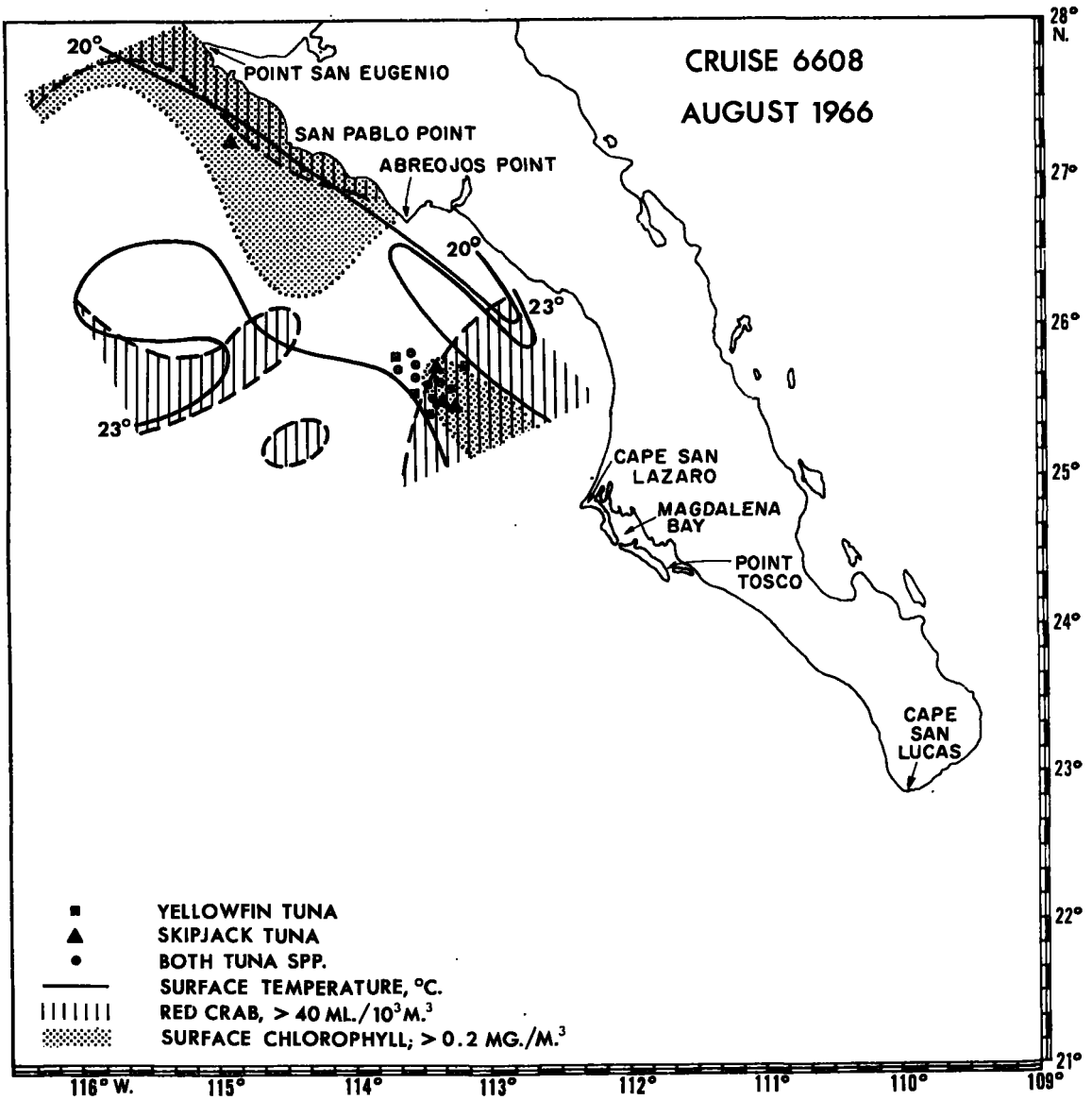

FIGURE 8.—Distributions of surface temperature, surface chlorophyll *a*, and red crabs for cruise 6608 and locations of contemporaneous tuna catches.

effort (nine boat-days) in one 1° square, bounded by lat. 26° and 27° N. and long. 114° and 115° W., took no tuna in the month of the cruise. According to figure 8, nearly all of this area was either colder than 20° C. (the northeastern corner) or had less than 40 ml./1,000 m.³ of red crabs at the time of the cruise. It would not, therefore, be expected to contain many tuna. Elsewhere the distribution of tunas at the time of the cruise is not known. Fishing effort was not significant in the area of high concentration of red crabs in the southwestern part of the cruise area, where temperature and food were suitable for tunas.

CRUISE TO–59–2

This cruise, made August 16–29, 1959, was in a warm year (see fig. 1), and the results represent conditions at a later stage in the year than those for the previous cruise. The cruise started farther south than the others in this series; the area immediately to the north was covered at the same period by CalCOFI cruise 5908 which yielded

TABLE 3.—*Concentrations of* Pleuroncodes planipes, *adults and juveniles (not larvae), in ml./10 ^{3}m.^{3} of water strained, on cruise 6608*

[Letters under kind of observation signify: Z, zooplankton haul; H, high-speed net haul between stations; S, seen in the water. Where concentrations were measured or estimated by more than one method, the highest concentration, corresponding to the first letter, is listed]

Station No.	Kind of observation	Concentration	Station No.	Kind of observation	Concentration	Station No.	Kind of observation	Concentration
		Ml./10^3 m.^{3}			*Ml./10^3 m.^{3}*			*Ml./10^3 m.^{3}*
1	Z	>40	23	Z	25	36	Z	113
1–2	H	>40	23–24	H	1,069	38	Z	6
2	Z	12	24	Z	7	41–42	H	17
5–6	H	392	24–25	H	334	43	Z	56
6	Z	13	25	S,Z	>40	43–44	H	426
7	Z	6	30	Z	28	44	S,Z	>40
14–15	H	1,353	31	S,Z	>40	45	Z	67
15	Z	13	31–32	H	818	45–46	H	468
16	Z	215	32	Z	20	46	Z	24
20	Z	7	32–33	H	12	(1)	H	5
21	Z	45	33–34	H	27	(1)	H	735
21–22	H	701	34	Z	14	(1)	H	1,762
22–23	H	1,044	35–36	H	58	(1)	H	14

[1] After station 47, on northbound track between lat. 26°30′ N. and 27°50′ N., at night.

temperature data (Scripps Institution of Oceanography, 1961), but no data on chlorophyll or red crabs. Cruise coverage and property distributions are shown in figures 9 and 10. Data on red crabs are given in table 4.

Surface temperatures were between 18° and 30° C. but the areas under 20° C. and over 28° C. were extremely restricted (fig. 10). The cold inshore region between Point San Eugenio and San Pablo Point probably represents upwelling at a very late stage. A large tongue or tongues of relatively cool water (less than 25° C.) ran offshore from the coastal upwelling area as shown for previous cruises. No such signs of relatively cool water were off Magdalena Bay, where upwelling probably ceases earlier than it does farther north.

Observations on surface chlorophyll *a* were fewer on this cruise than on the others. Concentrations were much lower than before—from 0.11 to 0.02 mg./m.^{3}, which is consistent with the indications of a further weakening of upwelling. Concentrations were at or above 0.1 mg./m.^{3} only at stations 20, 30, 37, 38, 41, and 42. The isogram of 0.05 mg./m.^{3} follows the 25° C. isotherm fairly well (fig. 10), so the offshore tongue of relatively cool water generally had a higher concentration of chlorophyll than the surrounding warmer water.

The area in which concentrations of red crabs exceeded 40 ml./1,000 m.^{3} was broadly congruent with the area of cool water and the area of highest surface chlorophyll. The isograms of these three properties tend to be displaced a little from each other, but otherwise they agree in considerable detail. There was an isolated patch of red-crab-rich water off Magdalena Bay; it was not cool, and chlorophyll was not sampled in this particular area.

About half of the tuna catches that were made at the time of the cruise were north of Abreojos Point, where data on chlorophyll and red crabs are lacking; temperatures were mostly over 20° C. The catches to the south of Abreojos Point all were from water over 20° C. and show the kind of association with chlorophyll and red crabs that was mentioned for cruise 6608. The tuna were not only on the edges of the biologically rich areas but in the cores of these areas as well. The areas of abundant forage, which on cruise TO–64–2 were too cold for tunas except at the edges, were warm enough for the fish to penetrate on this cruise. As before, tuna distribution was not determined (insignificant amount of fishing) in certain large areas, including some in which temperature and food conditions appeared highly suitable.

CRUISE TO–65–1

This cruise (figs. 11 and 12), which was in September 1965, represents a still later stage in the year, when the distribution of surface temperature gives no indication of any coastal upwelling. The lowest temperatures, between 20° and 21° C., were offshore and probably indicate California Current water. The highest temperatures were slightly over 28° C. Temperatures on part 2 of the cruise were about the same as on part 1. On CalCOFI cruise 6509, which extended into the northern part of the area near the end of cruise TO–65–1, sur-

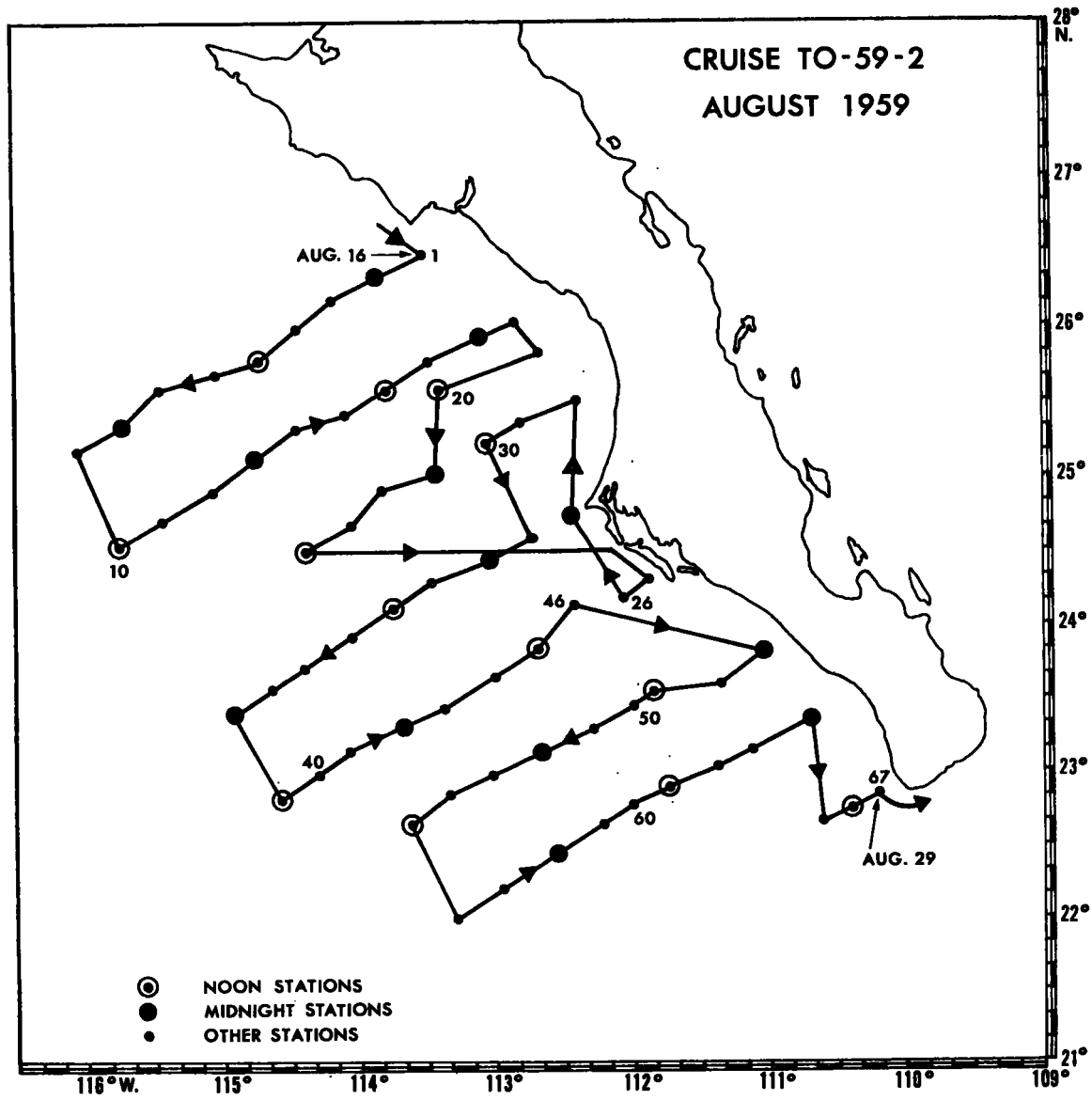

FIGURE 9.—Track and station positions for cruise TO–59–2.

face temperatures were about 1.5° C. lower in a few inshore localities, and elsewhere about the same as on TO–65–1 (Scripps Institution of Oceanography, 1967). Even these lower temperatures were over 20° C. and would not be expected to affect tuna distributions; therefore, all tuna occurrences for the whole period, September 8–25, 1965, have been given in figure 12. Data on red crab concentrations are given in table 5.

Surface chlorophyll *a* concentrations were all below 1.0 and ranged down to 0.02 mg./m.^{3}, although they were generally higher than on cruise TO–59–2. The 0.2 mg./m.^{3} isogram encloses the area of highest concentration, which is tonguelike and originates on the coast south of Point San Eugenio, as on previous cruises. It probably represents the biological result of a tongue of upwelled water which can no longer be distinguished from the surrounding water by its temperature. All stations inshore of this tongue and the following stations offshore had over 0.1 mg./m.^{3}: 4–6, 12, 13, 17, 23, 26–29, 32, and 36.

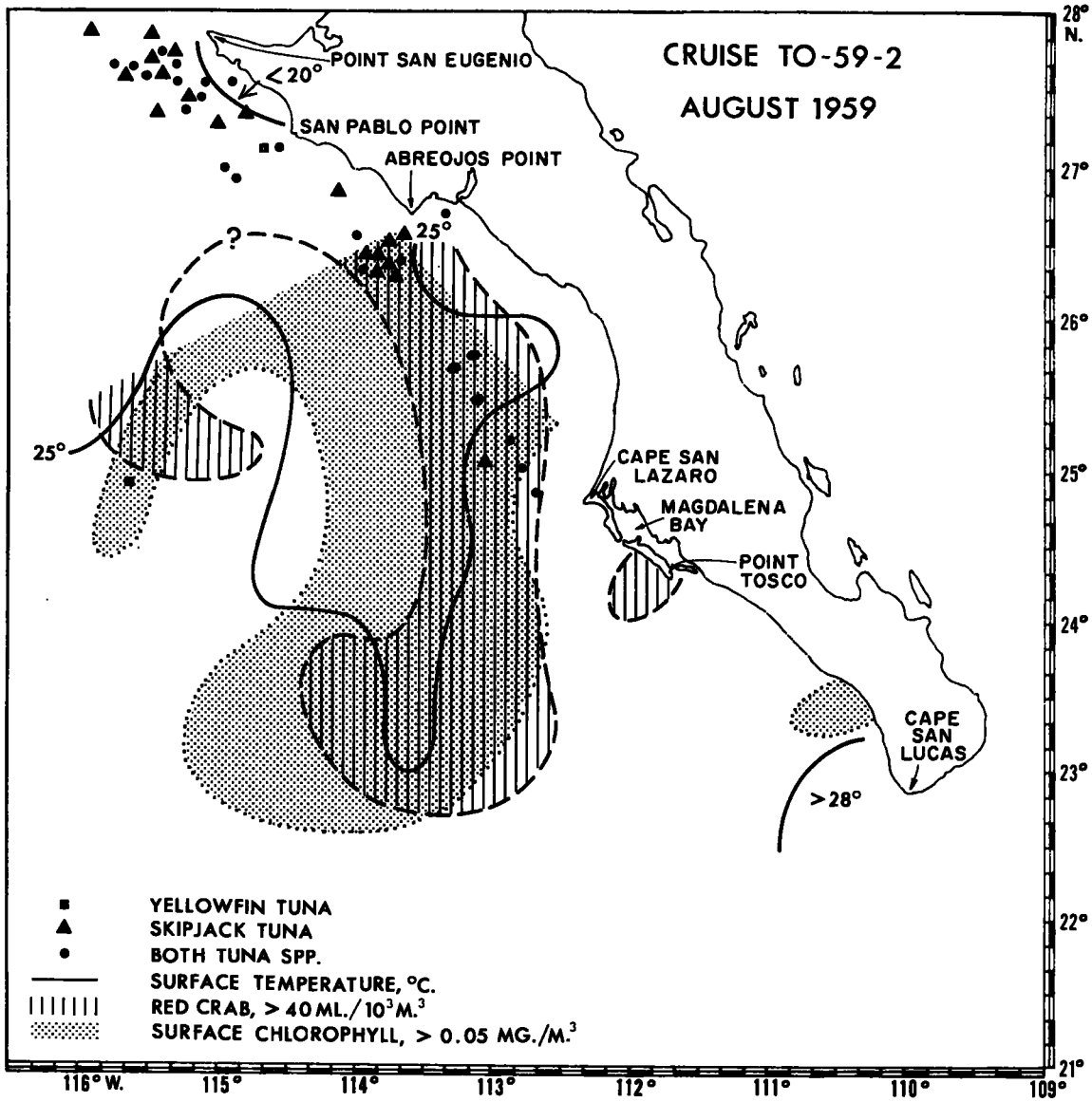

FIGURE 10.—Distributions of surface temperature, surface chlorophyll *a*, and red crabs for cruise TO–59–2 and locations of contemporaneous tuna catches.

The area where red crabs were over 40 ml./1,000 m.³ shows the same close but not exact correspondence with the chlorophyll-rich area that was found on previous cruises, and all the tuna catches were made in or very close to this area. The highest concentrations of carnivores (tuna), herbivores (red crabs), and plants (chlorophyll *a*) all were in the same restricted area. Because all temperatures were suitable for tunas, the tunas occurred, as before, not only around but through the food-rich areas.

CRUISE TO–66–1

The cruise period in the area of interest was November 4–21, 1966. The cruise (figs. 13 and 14) included stations with numbers below 15 and above 70, which were occupied on behalf of another investigator and were all north of lat. 28° N.

As I expected, conditions were much more uniform throughout the area on this cruise than on any of the others, because coastal upwelling had ceased. The only inshore pocket of cool water,

TABLE 4.—*Concentrations of* Pleuroncodes planipes, *adults and juveniles (not larvae), in ml./10³ m.³ of water strained, on cruise TO–59–2*

[Letters under kind of observation signify: M, micronekton haul; Z, zooplankton haul; H, high-speed net haul between stations; S, seen in the water. Where concentrations were measured or estimated by more than one method, the highest concentration, corresponding to the first letter, is listed]

Station No.	Kind of observation	Concentration
		Ml./10³ m.³
1	S	>40
2	Z,M	>40
5–6	H	2
6–7	H	4
7	Z	>40
8	M	176
8–9	H	35
9–10	H	3
11–12	H	1
13	M	42
13–14	H	26
15	Z	6
15–16	H	2
17–18	H	225
18	Z	>40
18–19	H	24
19–20	H	43
19–20	H	213
20	S,Z	>40
21	M	64
21–22	H	36
22–23	H	20
26	Z	158
26–27	H	15
26–27	H	16
27–28	H	8
28–29	H	6
30–31	H	8
30–31	H	1,158
31	Z	7
32	Z,M	229
32–33	H	158
33	Z	58
34	Z	9
35	Z	13
35–36	H	59
36	Z	6
38	M,Z	34
38–39	H	2
40–41	H	93
41–42	H	5
42	M	132
42–43	H	5
43–44	H	8
46–47	H	6
46–47	H	27
52	M	108
53	Z	128
53–54	H	495
54	Z	9
55	Z	8
57	Z	15
57–58	H	2
58	M,Z	20

which might have indicated upwelling, was a very small one off Point Tosco (21°–22° C.). Temperatures for the whole area were between 18° and 26° C. on part 1 of the cruise; on part 2, temperatures at reoccupied stations were only slightly (less than 1° C.) lower.

The range of chlorophyll *a* concentrations was about the same as on cruise TO–65–1, but their distribution was more uniform. Concentrations were over 0.1 mg./m.³ in most of the area as shown in figure 14. Concentrations were over 0.2 mg./m.³ at all stations north of lat. 26° 20′ N., and there only. Similarly, concentrations of red crabs were 40 ml./1,000 m.³ or higher in most parts of the cruise area (see table 6 for data). Finally, the recorded catches of tuna (all those for the period November 4–21) were scattered through the large area of suitable temperatures and abundant red crabs.

There was no opportunity to make a similar cruise closer to the end of the season for yellowfin and skipjack tunas off western Baja California, say in December or January. Such a cruise would probably have shown that the area available for the tunas had contracted because of the southward movement of isotherms, and a rather featureless distribution of the tunas—similar to that on cruise TO–66–1, associated with relatively uniform distributions of red crabs and chlorophyll *a*—in the area of suitable temperature.

OCEANIC PROPERTIES AND THE DISTRIBUTION OF TUNAS

The results of cruises TO–64–1, TO–64–2, 6608, and TO–59–2 all show the expected close agreement in detail between areas of relatively cool water that are attributable to upwelling and areas of relatively high surface chlorophyll *a*. The poor agreement between isograms of temperature and chlorophyll *a* in the northwestern portion of the cruise area shown in figure 6 is not necessarily an exception to the preceding statement, because the cool water may not represent upwelling there. The results of cruise TO–65–1 show a region of relatively high surface chlorophyll *a* in a locality and with a shape, which suggest an origin in upwelled water. No signs of upwelling appeared on cruise TO–66–1. The distributions of surface isotherms in space and time are consistent with previous information about upwelling off southern Baja California. Temperatures rise and chlorophyll *a* concentrations fall in the upwelling areas as the upwelling becomes weaker.

The results of all the cruises show rather close agreement in detail between the areas of relatively high surface chlorophyll *a* and the areas in which the concentration of red crabs is more than 40 ml./1,000 m³. The concentration of chlorophyll *a* which shows this agreement varies; on most of the cruises it was 0.2 or 0.1 mg./m³., but it was higher on cruise TO–64–1 and lower on cruise TO–59–2. The only complete lack of agreement appears in

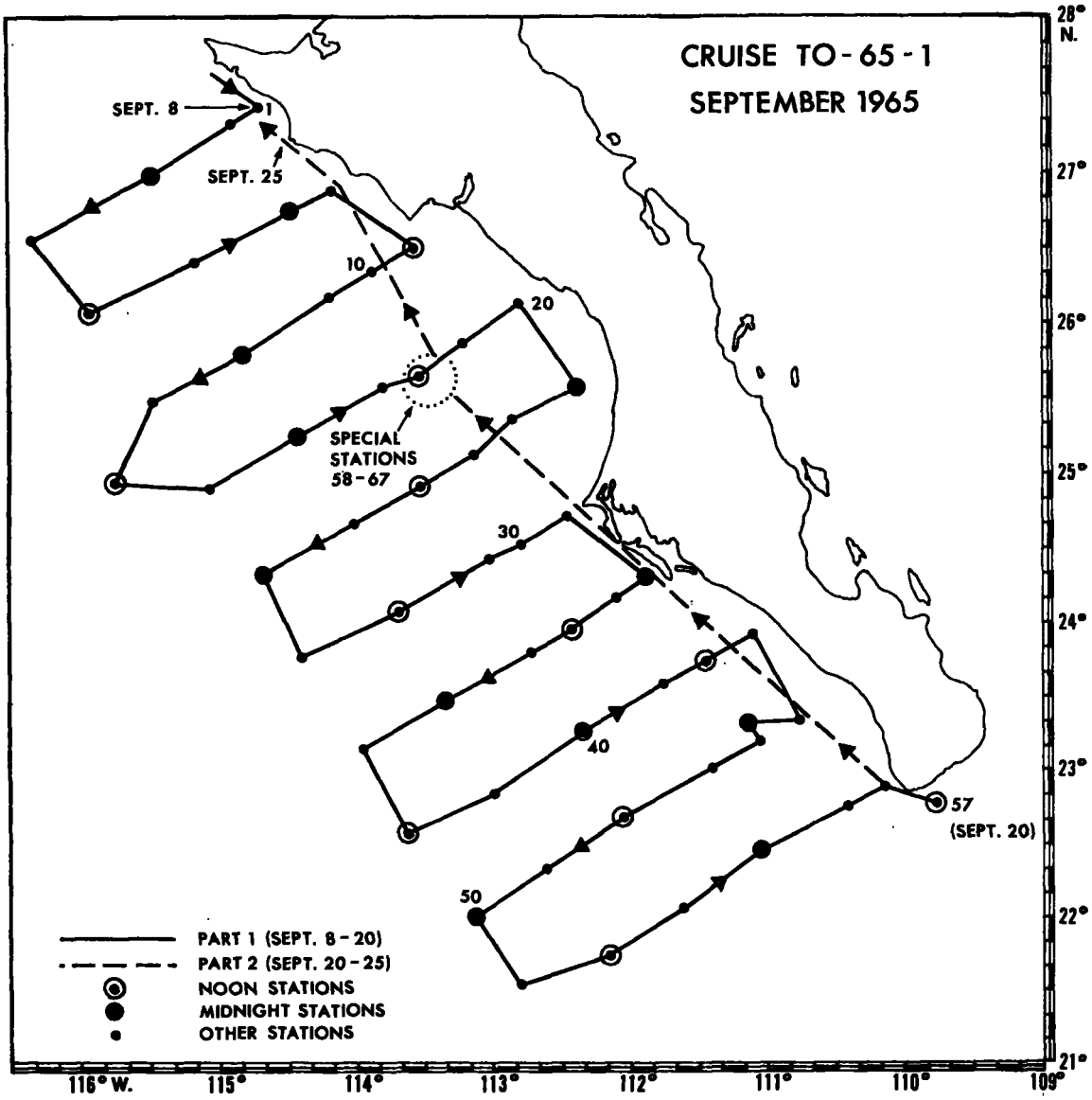

FIGURE 11.—Track and station positions for cruise TO-65-1.

the northwestern part of the cruise area shown in figure 6. Elsewhere in all the charts, agreement is fair to good. The area boundaries for the two properties seldom coincide, but they tend to lie close together and to have the same shape. Where the isograms of chlorophyll *a* follow those of temperature, all three properties—temperature, chlorophyll *a*, and red crabs—have a closely similar distribution (e.g., fig. 10).

The occurrence of red crab maxima with chlorophyll *a* maxima is not surprising because red crabs feed on phytoplankton, but the circumstances whereby they maintain aggregations in chlorophyll-rich areas are not altogether clear. On the one hand, the distribution data of Boyd (1967) and Longhurst (1967) indicate that the red crab can be swept away from the coast by the California Current during its pelagic phase. On the other hand, substantial numbers of this species occur in the benthos along the Continental Shelf and Slope (Boyd, 1967), and these individuals probably help to maintain pelagic concentrations in coastal areas by generating larvae and by ascending into the upper waters from time to time. Larvae are most

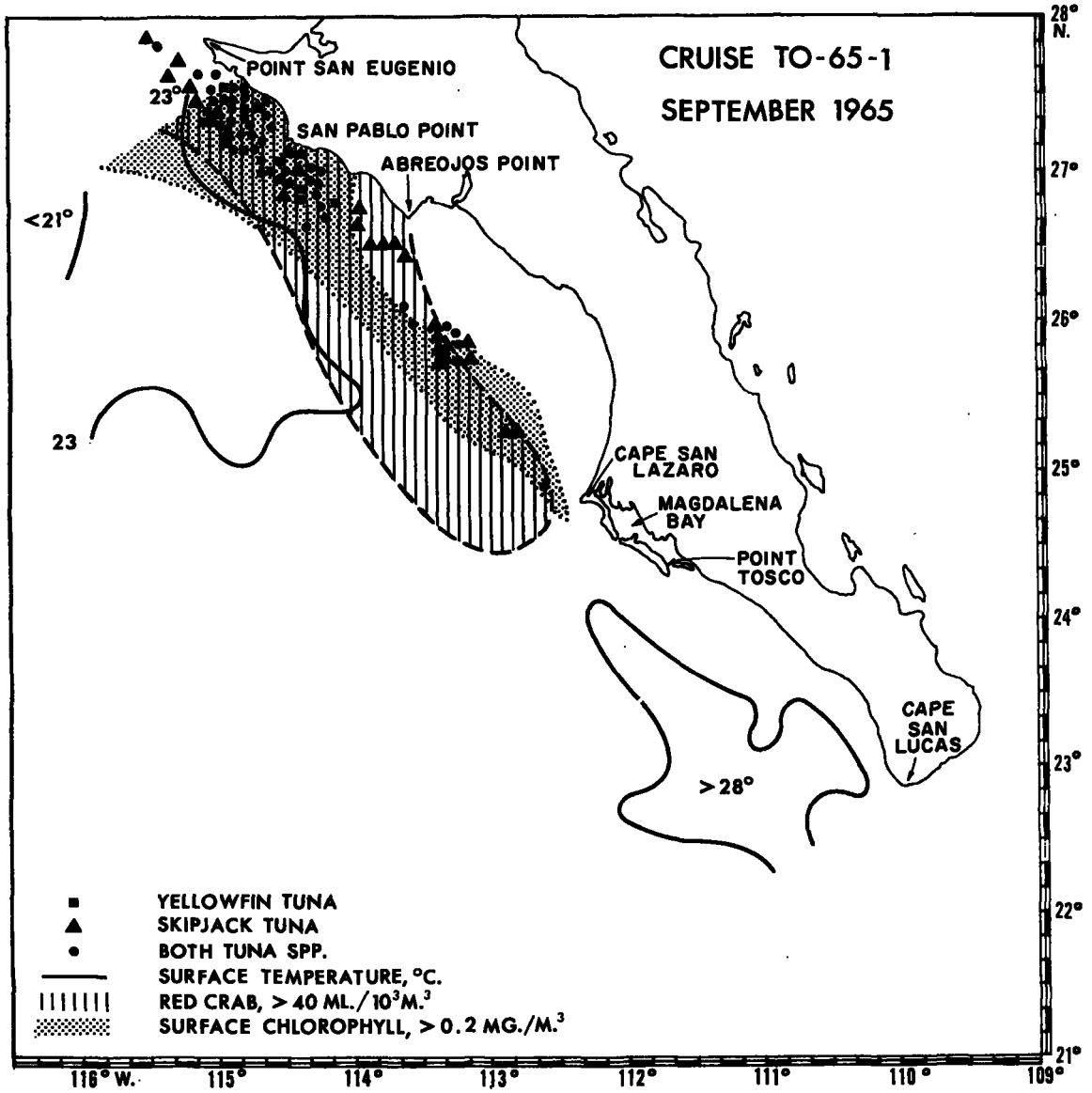

FIGURE 12.—Distributions of surface temperature, surface chlorophyll *a*, and red crabs for cruise TO–65–1 and locations of contemporaneous tuna catches.

numerous in inshore waters off the west coast of southern Baja California before and during the upwelling season, and benthic adults probably produce many of them (Longhurst, 1968a). The maintenance of pelagic aggregations is probably served also by the formation of inshore eddies after June (Wyllie, 1966). I assume that these processes, together with the animal's own appreciable mobility, maintain high concentrations in inshore areas where food (phytoplankton) is abundant; when food is scarce inshore red crabs presumably sink, disperse, or die.

The presence of red crab concentrations in cool water on some of the cruises results from the relation between chlorophyll *a* and upwelling, and is, therefore, not apparent on cruises TO–65–1 and TO–66–1. Longhurst (1967) showed that red crabs are practically eurythermal between about 9° and 28° C.

The data on tuna occurrence are all consistent with the hypothesized association with surface temperature (about 20° C. or more) and food sup-

TABLE 5.—*Concentrations of* Pleuroncodes planipes, *adults and juveniles (not larvae), in ml./10³m.³ of water strained, on cruise TO–65–1*

[Lettersunder kind of observation signify: M, micronekton haul; Z, zooplankton haul; H, high-speed net haul between stations; S, seen in the water; P, found in predator stomachs. Where concentrations were measured or estimated by more than one method, the highest concentration, corresponding to the first letter, is listed]

Station No.	Kind of observation	Concentration	Station No.	Kind of observation	Concentration	Station No.	Kind of observation	Concentration
		Ml./10³ m.³			*Ml./10³ m.³*			*Ml./10³ m.³*
2	Z	64	21–22	H	9	54	Z,M	3
3	M	1	22–23	H	15	(1)	P	>40
6	Z	32	26	M	22	60	Z	5
7	M	1	29	S,Z	>40	61	Z	55
7–8	H	500	36	Z	21	62	Z	3
8	Z	6	37	Z,M	12	63	Z	32
10	S,Z	>40				64	Z	3
11	Z	4	39	Z	5	65	Z	10
11–12	H	5	40	M,Z	4	66–4	Z	2
12	M,Z	3	41	Z	4	(2)	M	>40
12–13	H	5	42	Z	6	(3)	H	20
12–13	H	20	44	Z	2	(3)	H	158
15–16	H	5	45	M	<1	(3)	H	550
16	M,Z	5	49	Z	18	(3)	H	>40
16–17	H	342	49–50	H	15	(3)	H	2,500
18	Z	2	50	M,Z	24	(3)	H	100
20–21	H	18	51	Z	2	(3)	H	30

[1] Stomach contents of 3 yellowfin tuna (*Thunnus albacares*) at Thetis Bank.
[2] Series of night surface hauls with the large micronekton net near Uncle Sam Bank.
[3] After station 67, on northbound track between lat. 25°50′ N. and 26°40′ N., at night.

ply (40 ml./1,000 m.³ or more of red crabs), for all cruises except TO–64–1. On that cruise the tunas showed a tolerance of temperatures down to 17° C., but no lower in the presence of a larger food supply than that available to them at or over 20° C. Only one small area of abundant food (over 40 ml./1,000 m.³) and no area in which it was highly abundant (over 100 ml./1,000 m.³) had temperatures at and over 20° C.; food was highly abundant only at temperatures below 17° C. This difficulty (for the tunas) did not arise on any of the other cruises. On cruise TO–64–2 the edges of the areas of abundant food were warm enough for the tunas, which were found there and nowhere else. On cruises TO–59–2, TO–65–1, and TO–66–1 all parts of the food-rich areas were warm enough for tunas, which were, accordingly, widespread in them; they might have been found in still other places in the food-rich areas if the fishermen had searched there. On cruise 6608 the situation was partly like cruise TO–64–2 and partly like the other cruises. Except on cruise TO–64–1, no tuna were ever found more than 20 nautical miles (37 km.) from the charted boundaries of the food-rich areas.

From these results I may conclude that yellowfin and skipjack tunas aggregate in the areas of most abundant food where surface temperatures are about 20° (±1°) C. or over in waters west of Baja California, except at the beginning of their seasonal entry into those waters when they may occur at temperatures down to 17° C. Temperature determines range limits (penetration northward and toward the coast), and food supply determines distribution within the range limits. Because the principal food in this area is the red crab which occurs in areas rich in phytoplankton, tunas generally aggregate in or near the areas of highest surface chlorophyll *a*, provided that temperatures are suitable.

Because the distributions of temperature, chlorophyll *a*, and red crabs are all partly controlled by the seasonal coastal upwelling, at least through September, the same is true of the distribution of the tunas. Concentrations of tuna prey are much higher off western Baja California than anywhere else in the eastern tropical Pacific, where they are generally less than 10 ml./1,000 m.³ (Blackburn, 1968). These high values are a consequence of the upwelling and of the unusually short tuna food chain. The upwelling, however, furnishes an environment that tends to be too cold for yellowfin and skipjack tunas in spite of its biological richness, and this physical feature is decisive. The tunas do not enter the area and exploit the rich food supply until temperatures begin to rise. They then aggregate around the edges of the large tongues or patches of food and gradually penetrate into the cores of those areas as they become warm. Later the distribution of both the food and the tunas

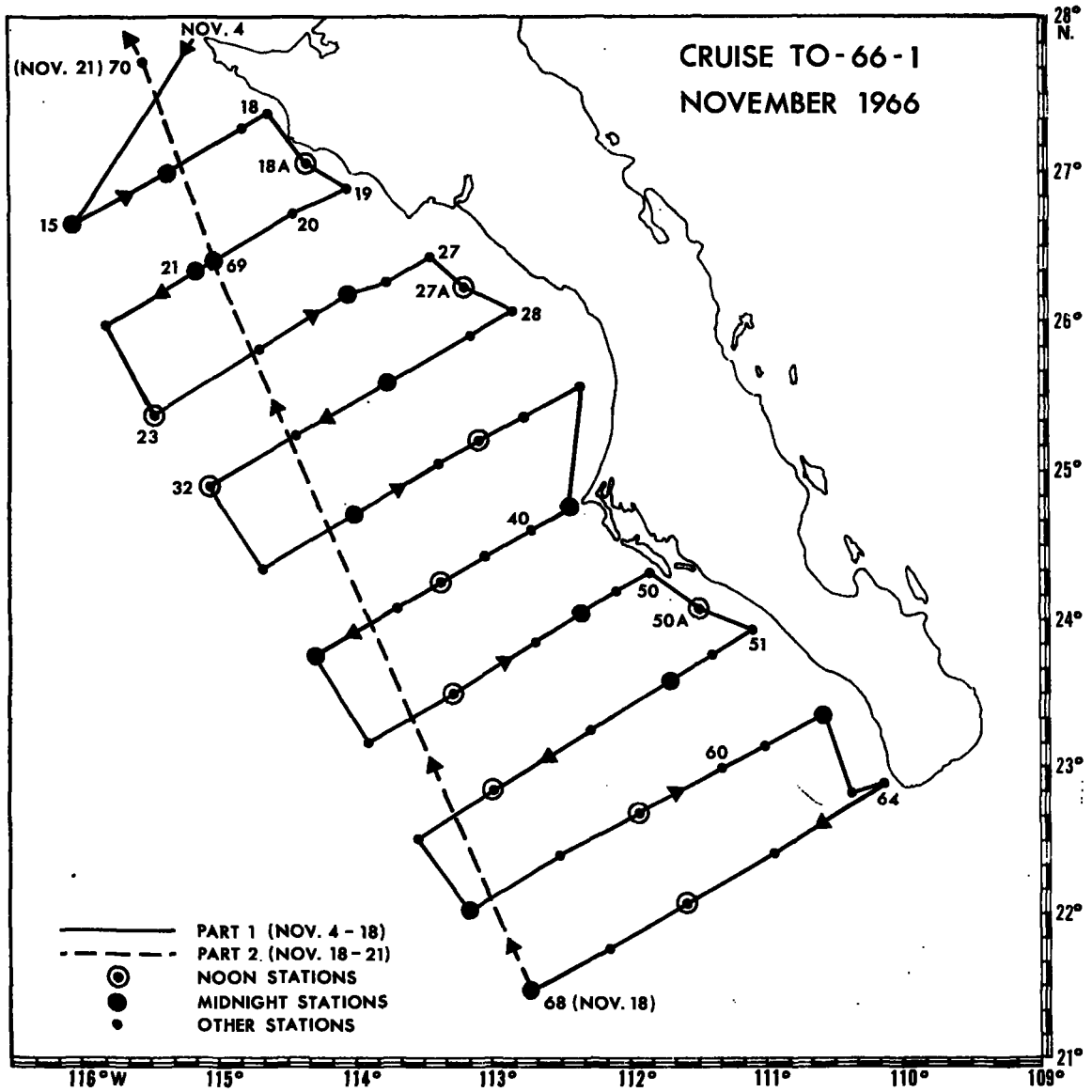

FIGURE 13.—Track and station positions for cruise TO-66-1.

becomes rather uniform in areas of suitable temperature, and finally the physical environment again becomes unsuitable with the start of winter cooling. The supply of pelagic red crabs remains fairly high throughout the year (Longhurst, 1967; Blackburn, 1968; and this paper).

The foregoing interpretation of the tuna distribution data might be criticized on two grounds. One is that nearly all the tuna catches shown in the charts were within 100 nautical miles (185 km.) of the coast, although suitable environmental conditions occurred much farther offshore on some of the cruises (see figs. 8 and 10), as well as in the inshore areas where the catches were made. Charts of IATTC data from the commercial fishery for many years, compiled by Joseph and Calkins (1969), show clearly that most of the fishing effort in the Baja California area is expended and most of the catch of both species taken within about 100 nautical miles of the coast. This situation is understandable because the tuna are associated with upwelling, which is a coastal process, and fishermen generally do not operate farther offshore than is necessary to make good catches. On

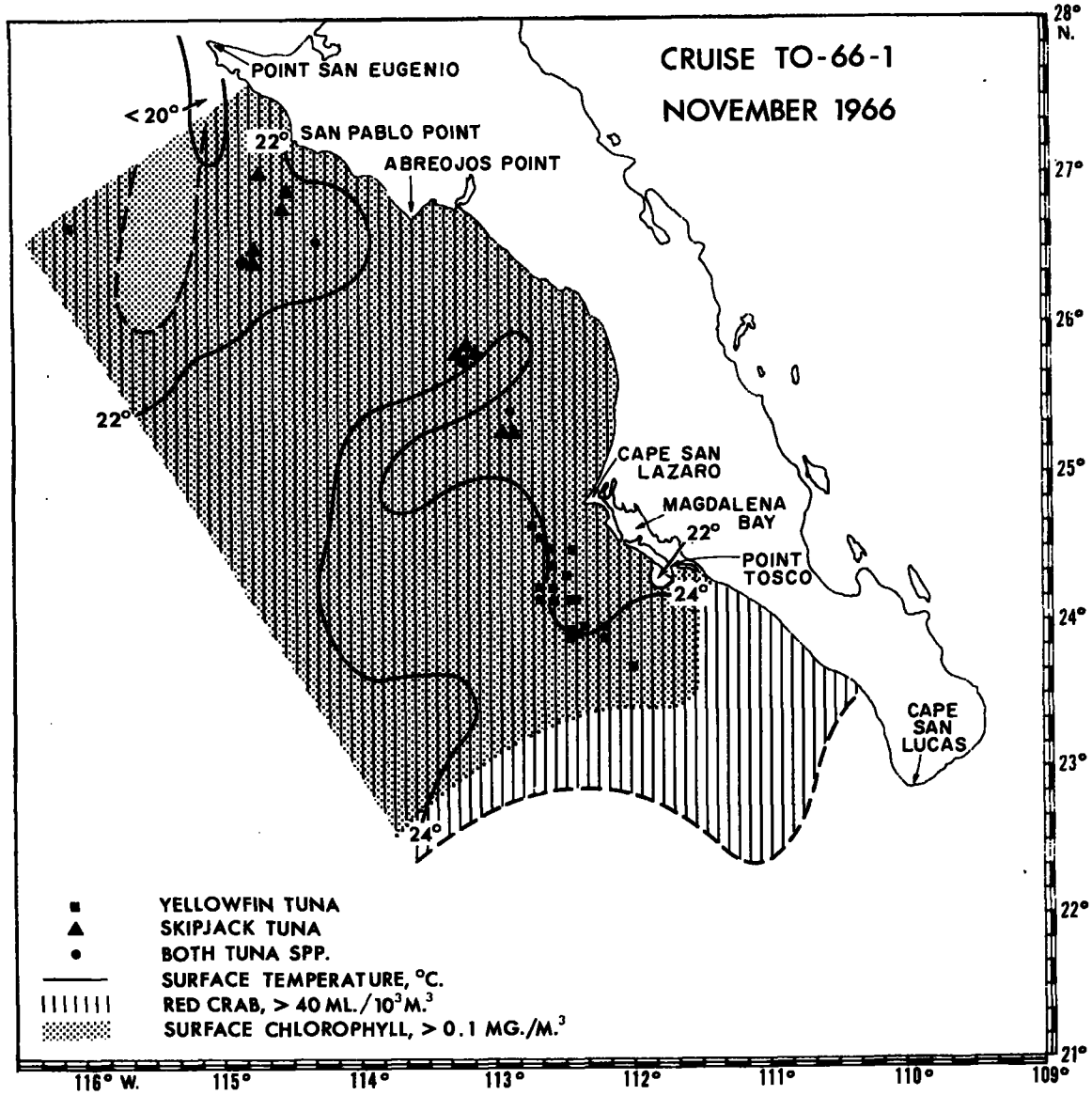

FIGURE 14.—Distributions of surface temperature, surface chlorophyll *a*, and red crabs for cruise TO–66–1 and locations of contemporaneous catches.

the other hand, the IATTC charts show that yellowfin and skipjack tunas are sometimes sought and captured offshore, for instance at Alijos Rocks, about 150 nautical miles (278 km.) from the coast (fig. 2), and even about 1° of longitude to the west of that locality. Nothing suggests that these offshore tuna are not aggregated in food-rich areas of suitable temperature in the same way as the inshore tuna. Furthermore, one definite record of an offshore commercial tuna catch appears to be associated with a tongue of food-rich water (fig. 10). This catch was at Alijos Rocks on cruise TO–59–2. The only other cruise in the present series which yielded information about properties at Alijos Rocks was TO–65–1 (see fig. 11, station 14). On that occasion, no tongue of biologically rich water reached the Rocks area, concentrations of chlorophyll *a* and red crabs were low, no tuna were seen or caught while the scientific party was fishing at the Rocks, and no commercial catches were recorded there during the cruise period.

The other possible objection to the model of

TABLE 6.—*Concentrations of* Pleuroncodes planipes, *adults and juveniles (not larvae), in ml./10³m.³ of water strained, on cruise TO–66–1*

[Letters under kind of observation signify: M, micronekton haul; Z, zooplankton haul; H, high-speed net haul between stations; S, seen in the water. Where concentrations were measured or estimated by more than one method, the highest concentration, corresponding to the first letter, is listed]

Station No.	Kind of observation	Concentration	Station No.	Kind of observation	Concentration	Station No.	Kind of observation	Concentration
		Ml./10³ m.³			*Ml./10³ m.³*			*Ml./10³ m.³*
15	S	>40	33–34	H	5,238	50	S,Z	>40
16	M	<1	34	S,Z,M	>40	52–53	H	43
17	Z	6	34–35	H	720	53	S, Z,M	>40
18A	Z	12	35	Z	7	53–54	H	25
20	S,Z	>40	36	Z	35	53–54	H	87
20–21	H	23	37	Z	7	56	Z	>40
21	S,Z,M	>40	38–39	H	20	57	M	<1
21–22	H	2	39	Z	41	59	Z	7
23–24	S	>40	39–40	H	13	60	S	>40
24	Z	7	40	M,Z	67	61	Z	57
24–25	H	20	41	Z	7	62	Z	50
25	M,Z	>40	42	Z	7	63	Z	7
25–26	H	53	43	S,Z	>40	65	S	>40
26	Z	27	43–44	H	73	68	Z	>40
27	Z	18	44	Z,M	19	(1)	H	233
29	Z	26	45	S,Z	>40	(1)	H	70
29–30	H	37	46	Z	13	(1)	H	150
30	S,Z,M	>40	47	Z,S	>40	(1)	H	82
30–31	H	704	48	M,Z	144	69	S,Z	>40
30–31	H	792	48–49	H	87	(2)	H	>40
33	S,Z	>40	49	Z	205			
33–34	H	>40	49–50	H	260			

[1] After station 68, on northbound track between lat. 23°40′ N. and 25°30′ N., at night.
[2] Immediately after station 69, on northbound track, at night.

tuna distribution offered in this paper is that many people who are acquainted with the Baja California fishery consider that yellowfin and skipjack tunas are distributed in relation to the banks shown in figure 2 and that abundance is higher at the banks than elsewhere, except when temperatures are low. No publications clearly demonstrate this relation as far as Baja California is concerned, and no studies off Baja California or elsewhere show conclusively the nature of any "bank effect" which might be attractive to tunas. In fact, only one such study has been attempted and the results were inconclusive (Bennett and Schaefer, 1960, at Shimada Bank in the eastern tropical Pacific). Nevertheless, belief in some kind of favorable bank effect upon tunas is so widespread that it must be considered here.

The tuna catches charted in figures 4, 6, 8, 10, 12, and 14 may be compared with the bank positions in figure 2. Many of the catches were made at or very near banks; they can be classified into two groups. All of those for the periods of cruises TO–64–2, 6608, TO–59–2, and TO–65–1 were in or close to tongues or patches of upwelled water, which either enveloped or touched the banks. None of the catches in the periods of cruises TO–64–1 and TO–66–1 were associated with upwelled water. On TO–64–1 no such water was warm enough for the tunas to enter, and on TO–66–1 there was none at all. The charts show also that many catches were in areas of upwelled water which were not close to banks, except on cruises TO–64–1 and TO–66–1.

When upwelled water of coastal origin extends over banks, it provides a ready explanation not only for the catches of tuna on banks (and at Alijos Rocks, as noted above) but also for the catches made between the banks. The unspecified bank effect may exist independently of the upwelling effect, but it is not required to explain the tuna distributions. If a bank effect exists, it is probably small in relation to the upwelling effect, and the banks are probably more suitable for tuna when upwelled water reaches them (providing it is not too cold) than when it does not. An observation from Uncle Sam Bank, which is very frequently visited by fishermen during the tuna season, is pertinent. Surface temperature charts for CalCOFI cruises 6007–8 (July 26 to Aug. 13, 1960, in the area of interest) and 6008 (Aug. 20–22, 1960) both show tongues of cool water (but over 20° C.) protruding offshore from the northern upwelling area. On the earlier cruise the tongue lay considerably west of Uncle Sam Bank, but on the later cruise it had changed its position and enveloped the bank (Scripps Institution of Oceanography, 1962a, 1962b). No tuna catches were recorded near the bank during the first cruise period.

but some were recorded there during the second period.

On the other hand, tuna aggregations upon banks which are not affected by upwelled water might be primarily attributable to a bank effect. Further work is needed to establish the reality of the bank effect and to explain it if it does exist. Obviously, this research should be attempted in a situation where upwelling is not likely to interfere with the bank environment, such as one of the offshore southern banks toward the end of the tuna season. In the meantime, it is reasonable to assume that some feature of banks makes them slightly more attractive to tunas than other areas when temperatures are suitable, and that this feature affects tuna distributions in situations where upwelled water does not interfere. Off Baja California these situations are probably most common in the southern part of the area, where upwelled water does not seem to reach far offshore; at the beginning of a tuna season when tuna are unable to enter upwelled water; and after all upwelling has ceased.

Fishermen often make an additional observation that tunas aggregate near boundaries between blue and green water. Some of the results of this study, especially for cruise TO–64–2, are consistent with that opinion. Blue water would frequently have suitable temperature but not much food; green water may contain suitable food but be too cold. Tuna would be expected to aggregate at the boundary under those circumstances.

The relation of tuna to the Cape San Lucas front was discussed under cruise TO–64–1. Evidence is lacking that this particular front has any effect upon tunas independent of the tuna-limiting temperatures that may occur in it. Low temperature tends to be limiting, whether located in the front or not, and no other feature of the front seems to have any effect upon the tunas.

If the area west of Baja California could be thoroughly and frequently monitored for surface temperature and surface chlorophyll *a* during a tuna season, it would be possible to specify areas in which aggregations of yellowfin and skipjack tunas would be expected—including offshore areas which fishermen might not otherwise visit—and those in which tuna would not be expected. This work could perhaps be done from ships, which already yield much data on surface temperature and could be equipped to yield data on surface chlorophyll *a* (Lorenzen, 1966). The chlorophyll equipment would be costly, however (about $2,000 per ship), and require careful maintenance aboard ship. Overflying aircraft or satellites offer another possibility. They would probably yield much more useful data than ships except in cloudy situations. Methods of measuring surface temperature from sensors above the ocean already exist, and measurement of surface chlorophyll is said to be feasible (Duntley, 1965). Obviously, the chlorophyll information could assist in mapping distributions of other useful organisms besides tuna—for example, the red crab itself, a possible human resource (Longhurst, 1968b), and other herbivores. Temperature data alone would be insufficient to specify distributions of tuna or red crab.

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Many people assisted in the work reported in this paper. The Inter-American Tropical Tuna Commission supplied data on tuna catches, and the following persons commented on the first draft: G. Flittner, J. Joseph, W. Klawe, A. Longhurst, C. Orange, R. Owen, W. Thomas, F. Williams, and B. Zeitzschel.

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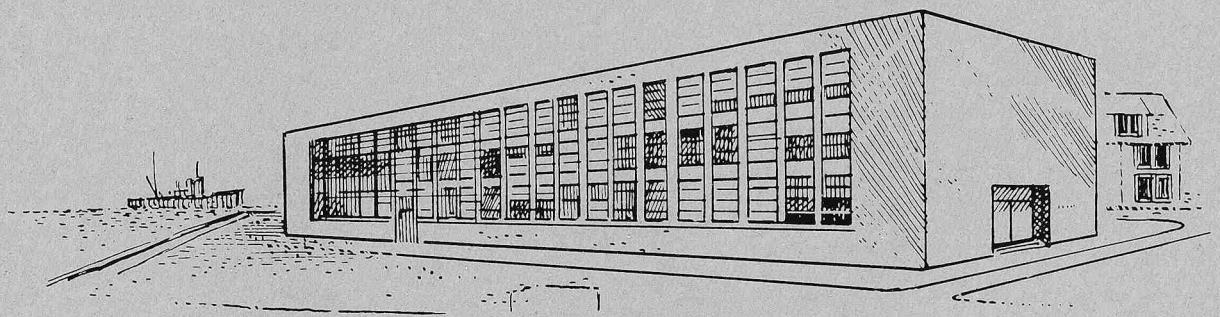

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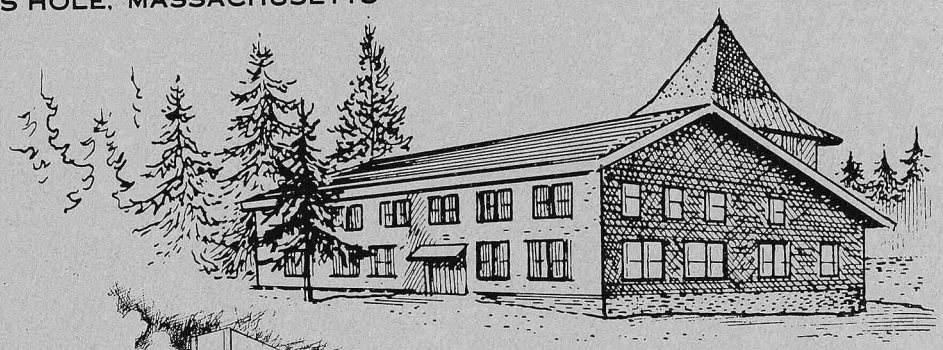

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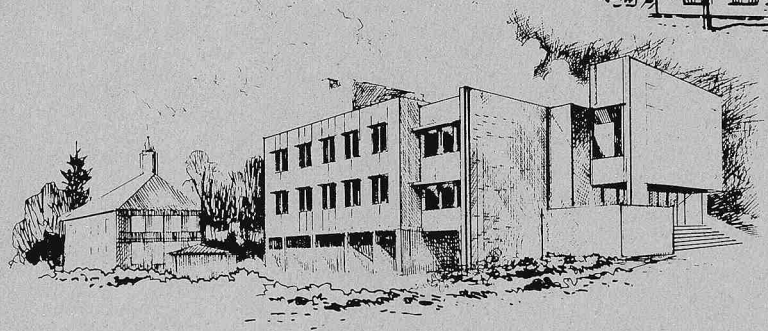

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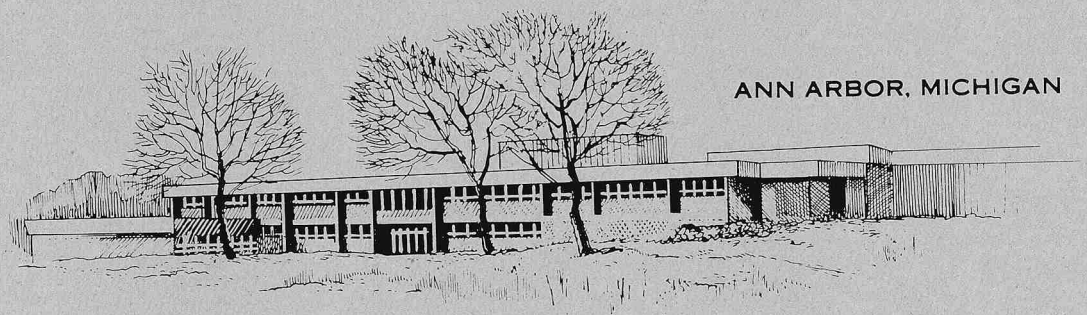

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Washington, D.C.

February 1971

YOUNG OF THE ATLANTIC SAILFISH, *ISTIOPHORUS PLATYPTERUS*[1]

BY JACK W. GEHRINGER, *FISHERY BIOLOGIST*
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ABSTRACT

One hundred fifty-four Atlantic sailfish, 26.1 to 216 mm. in standard length, were dip netted on cruises of the Bureau of Commercial Fisheries charter vessel *Silver Bay* off the south Atlantic Coast of the United States in 1960 and 1962. This group of specimens (larger than any previously available collection of sailfish of similar size) was examined to determine changes during development. Thirty-four eastern Atlantic specimens 13.8 to 238 mm. in standard length that were dip netted in 1968 on a cruise of the Bureau's vessel *Undaunted* in the Gulf of Guinea were compared with the specimens from the western Atlantic.

Five western Atlantic specimens are illustrated. Loss of larval characteristics and development of fins and fin rays and pigmentation are discussed. Correlations of numbers of fin rays and statistics describing relationships of measurements of selected body parts for western Atlantic specimens are presented. Principal differences between eastern and western Atlantic specimens are the slightly longer pectoral fin, snout, and head in eastern Atlantic specimens.

Collections of the young stages of Istiophoridae that include a sufficient number of larvae and juveniles for detailed studies of developmental stages are rare. The literature on young Atlantic sailfish, *Istiophorus platypterus* (Shaw and Nodder),[2] is primarily on small larvae and has information on only 21 specimens longer than 25 mm. SL (standard length)—(Voss, 1953, 4 specimens 29.5–208 mm.; Gehringer, 1957, 16 specimens 27.4–101 mm.; and de Sylva, 1963, 1 specimen, 167 mm.).

This paper is based primarily on a collection of 154 sailfish from the western Atlantic Ocean, 26.1 to 216 mm. SL. They were collected at dip net and nightlight stations on cruises of the BCF (Bureau of Commercial Fisheries) charter vessel *Silver Bay* off the southeastern coast of the United States in June and July 1960 and September and October 1962. Subsequent to my examination of the western Atlantic specimens and preparation of a draft of a manuscript describing them, I examined 34 specimens, 13.8 to 238 mm. SL (all but 1 over 25 mm. SL), collected by dip net at nightlight stations on a cruise of the BCF vessel *Undaunted* in the Gulf of Guinea, off the west coast of Africa, in April 1968.

For western Atlantic specimens I include detailed line drawings of a developmental series, statistics showing the relationships of measurements of selected body parts, and discussions of dorsal and anal fin rays and changes during their development. I compare eastern and western Atlantic specimens of similar size and include in my discussion of western Atlantic material those variations I found in eastern Atlantic material.

METHODS AND DATA

MEASUREMENTS

Measurements were made with dial calipers calibrated in 0.1-mm. units and are recorded to the nearest 0.1 mm. if less than 100 mm. or to the nearest millimeter if 100 mm. or greater.

DEFINITIONS OF TERMS

I consider all specimens in this study to be juveniles, by definition of the juvenile stage as sexually immature specimens whose numbers of fin rays are within the ranges for the adult.

Measurements

Standard length, head length, snout length, pectoral and pelvic fin lengths, eye diameter, and

[1] Contribution No. 95 from the Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Ga. 31520.

[2] In using the name *Istiophorus platypterus* (Shaw and Nodder), I follow Morrow and Harbo (1969).

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pterotic and main preopercular spine lengths are as defined by Gehringer (1957). Trunk length is the distance between the posteriormost margin of the orbit and anterior point of emergence of the upper keel on the caudal peduncle on specimens 85 mm. SL or longer (de Sylva, 1957). On specimens smaller than about 85 mm. SL, which lack keels, the posterior point for this measurement is the insertion of the leading edge of the finfold of the dorsal lobe of the caudal fin. This point is directly above the anterior edge of the caudal keel on larger specimens. Body length is the distance between the tip of the mandible and the tips of the midcaudal fin rays (Rivas, 1956). Body depth is a vertical measurement at the insertion of the first pelvic fin ray. Pelvic fin to anal fin is the distance between the insertion of the first pelvic fin ray and the insertion of the first anal fin ray.

Fin Rays

The dorsal and anal fins are single fins in the larval and juvenile stages, but in the adult the terminal six or seven rays of both fins are separated from anterior portions of these fins to form second dorsal and anal fins. The fins are not divided in the largest specimens in this study, 216 to 238 mm. SL, although the anal fin is nearly divided. Even on my smallest western Atlantic specimen (26.1 mm. SL), the shape and size of the terminal six or seven rays distinguish them from the few, less robust, more widely spaced rays immediately ahead of them (which are overgrown with tissue in the adult). I recorded ray counts separately for the anterior and posterior portions of both dorsal and anal fins. The terminal ray in the dorsal and anal fins though divided to its base, is recorded as one ray.

STUDY MATERIAL

Western Atlantic specimens are from *Silver Bay* cruises, all taken by dip net at the surface, under a nightlight: Sta. 2139: 29°55′ N., 80°38′ W. (about 35 nautical miles E. of St. Augustine, Fla.); 2045–2245 hours, June 12, 1960; 33 m., surface temperature 25.6° C.; 3 specimens, 81.9 to 155 mm. SL. Sta. 2172: 35°00′ N., 75°19′ W. (about 20 nautical miles SE. of Cape Hatteras, N.C.); 2200–0250 hours, July 18–19, 1960; 146 to 366 m., surface temperature 27.3° C.; 10 specimens, 67.1 to 216 mm. SL. Sta. 2201: 34°34′ N., 75°40′ W. (about 50 nautical miles E. of Cape Lookout, N.C.); 0030–0400 hours, July 24, 1960; 146 to 165 m., surface temperature 28.9° C.; 135 specimens, 26.1 to 167 mm. SL. Sta. 2268: 32°36′ N., 78°30′ W. (about 70 nautical miles E. of Charleston, S.C.); 0115–0300 hours, July 29, 1960; 190 to 198 m., surface temperature 28.9° C.; 4 specimens, 37.1 to 91.1 mm. SL. Sta. 4326: 28°32′ N., 80°03′ W. (about 25 nautical miles E. of Cape Kennedy, Fla.); 2310–0115 hours, September 3–4, 1962; 70 m., surface temperature 27.8° C.; 1 specimen, 137 mm. SL. Sta. 4403: 28°56′ N., 80°25′ W. (about 30 nautical miles N. of Cape Kennedy, Fla.); 2345–0145 hours, October 4–5, 1962; 24 m., surface temperature 28.9° C.; 1 specimen, 169 mm. SL.

Eastern Atlantic specimens are from *Undaunted* Cruise 6801, all taken by dip net at the surface, under a nightlight: Sta. 126: 00°11′ S., 08°39′ E.; 2000–2400 hours, April 16, 1968; 1,080 m., surface temperature 28.8° C.; 1 specimen, 104 mm. SL. Sta. 132: 00°38′ N., 07°21′ E.; 1900–2400 hours, April 17, 1968; 2,664 m., surface temperature 29.6° C.; 3 specimens, 29.9 to 49.8 mm. SL. Sta. 138: 01°20′ N., 07°55′ E.; 2030–0230 hours, April 19–20, 1968; 2,400 m., surface temperature 28.6° C.; 13 specimens, 13.8 to 147 mm. SL. Sta. 152: 02°25′ N., 06°29′ E.; 2200–0200 hours, April 23–24, 1968; 1,520 m., surface temperature 28.9° C.; 1 specimen, 47.9 mm. SL. Sta. 158: 04°52′ N., 05°34′ E.; 0000–0215 hours, April 25, 1968; 240 m., surface temperature 28.8° C.; 16 specimens, 29.5 to 238 mm. SL.

All study material is cataloged in the fish collections of BCF Tropical Atlantic Biological Laboratory, Miami, Fla.

DEVELOPMENT AND GROWTH

My discussion of changes during development and growth concerns loss of larval characteristics, pigmentations, fin rays, and relations of measurements of various body parts.

LOSS OF LARVAL CHARACTERISTICS

Within the size range represented here, head spines are lost, scales undergo changes, caudal keels develop, and changes occur in the dorsal, anal, and pelvic fins.

Head Spines

In an earlier paper on the Atlantic sailfish (Gehringer, 1957), I reported pterotic and preopercular spines on a 101-mm. SL specimen. Voss

(1953) stated that these spines were not present on a 208-mm. SL specimen. In the present large series of western and eastern Atlantic sailfish, pterotic spines are present only as traces on some fish as short as 100 mm. SL, are present on all fish up to 150 mm. SL, and are absent on specimens longer than 150 mm. SL. Preopercular spines are present on all specimens but the largest, 216 to 238 mm. SL—they are probably lost at about this size.

Scales

Scale spines are first discernible on the dorsolateral surface of the body on sailfish about 30 mm. SL. Specimens about 50 mm. SL have spines on the cheeks and most of the body, except for the area on the side covered by the depressed pectoral fin and on the back along the anterior portion of the dorsal fin. Scales on the largest specimens, 216 to 238 mm. SL, are cycloid and differ from the illustration and description of scales on a 101-mm. fish (Gehringer, 1957) as follows: shape more elliptical than round, spine relatively shorter and weaker, and concentric ridges greater in number. On all specimens longer than 30 mm. SL the spine tips protrude through the skin and give a feeling of roughness.

Development of Caudal Keels

Two keels on each side, extending from the base of the caudal fin onto the caudal peduncle, develop at about 84 to 92 mm. SL. The smallest sailfish with keels is 83.8 mm. SL, and the largest without keels is 91.4 mm. SL. The upper keel apparently develops first as it is the only one present on the few fish 85 to 90 mm. SL with but one keel.

Development of Dorsal and Anal Fins

As discussed under definitions of terms, the last six or seven rays of both dorsal and anal fins form distinct second fins in the adult. The dorsal and the anal fins on all specimens in the present series are single and continuous. On larger specimens the few anal rays immediately forward of the terminal six or seven rays are small and weak; these rays are weak and overgrown with skin in the adult. Dorsal rays in this relative position are not so weak, but are less robust than those immediately ahead or behind which do not become overgrown with skin. On most specimens over 80 mm. SL, the distal portion of the anal ray immediately ahead of the terminal six or seven rays is depressed, overgrown with tissue, and nearly adnate to the base of the succeeding ray.

Pelvic Fin

The first and second rays of the pelvic fin, which in the adult are fused into one robust bony ray, are nearly fused on the largest specimens, 216 to 238 mm. SL—the first ray appears as a short, triangular-shaped segment of the leading edge of the second ray. The third ray is separate and distinct at all sizes.

PIGMENTATION

Pigmentation of Atlantic sailfish larvae, juveniles, and adults has been described by several authors, including Voss (1953), Gehringer (1957), Robins and de Sylva (1963), and de Sylva (1963). My comments here on pigmentation of fins and body bars supplement these accounts for specimens 26 to 238 mm. SL and apply to both eastern and western Atlantic specimens.

Fins

The pectoral fins are clear except for a few melanophores at the bases of the first few rays on the largest specimens.

The pelvic fins are lemon-yellow with a few melanophores on the membrane between the second and third rays on sailfish over 155 mm. SL.

Pigment on the anterior portion of the dorsal fin is uniformly dusky to dark except for two to several large, dark spots scattered in a nonuniform pattern over the fin (figs. 1–5). On some fish the first few dorsal rays are less densely pigmented than the rest of the fin. Pigment extends posteriorly on the fin to the 34th to 40th ray—the last few rays of the anterior portion have no pigment. The posterior portion (terminal six or seven rays) of the fin is clear except for pigment on the bases of the fin rays and fin membrane on specimens longer than about 135 mm. SL.

The anal fin is clear on all specimens.

The smallest sailfish with pigment on the caudal fin is 44.2 mm. SL; the largest without pigment on the caudal fin is 51.7 mm. SL. A group of a few melanophores is present on the lower lobe of the caudal fin of a series of fish 44.2 to 60.0 mm. SL, and a similar group of melanophores is also on the upper lobe of a series of specimens 50.0 to 64.0 mm. SL. The melanophores are coalesced into blotches on several fish 53.2 to 67.0 mm. SL, and, though

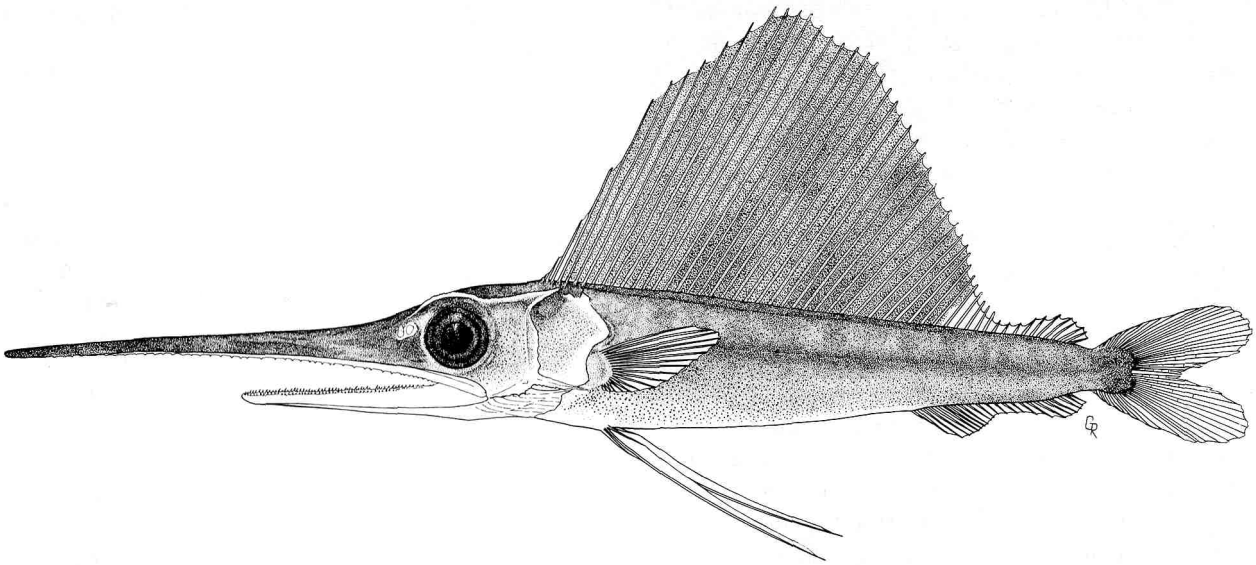

FIGURE 1.—Juvenile sailfish, 37.1 mm. standard length, *Silver Bay* Sta. 2268.

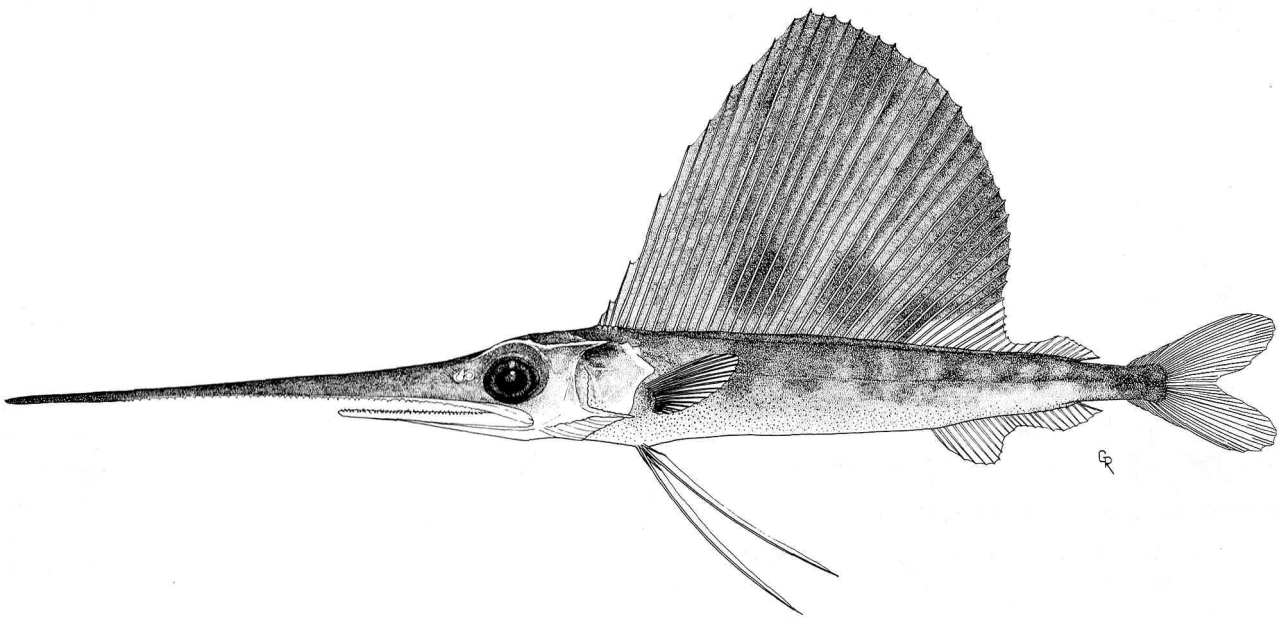

FIGURE 2.—Juvenile sailfish, 55.1 mm. standard length, *Silver Bay* Sta. 2268.

larger and covering more of the fin lobes, the blotches are distinct on a series of specimens 101 to 119 mm. SL. On a 190-mm. SL sailfish, pigment spreading posteriorly from the base of the fin joins that spreading anteriorly on the lobes and covers the fin except for the distal half of the middle seven caudal rays and ray membrane, which remain clear. On the largest specimens, 216 to 238 mm. SL, the clear area of the middle part of the caudal fin is reduced to the distal third of the middle six caudal rays and ray membrane, the lobes of the caudal fin are dusky, and the tissue covering the bases of the rays is densely pigmented.

Body Bars

Pigment on the sides of the body is concentrated in five to seven bars on fish of about 30 mm. SL. Bars are not discernible on smaller specimens. Sail-

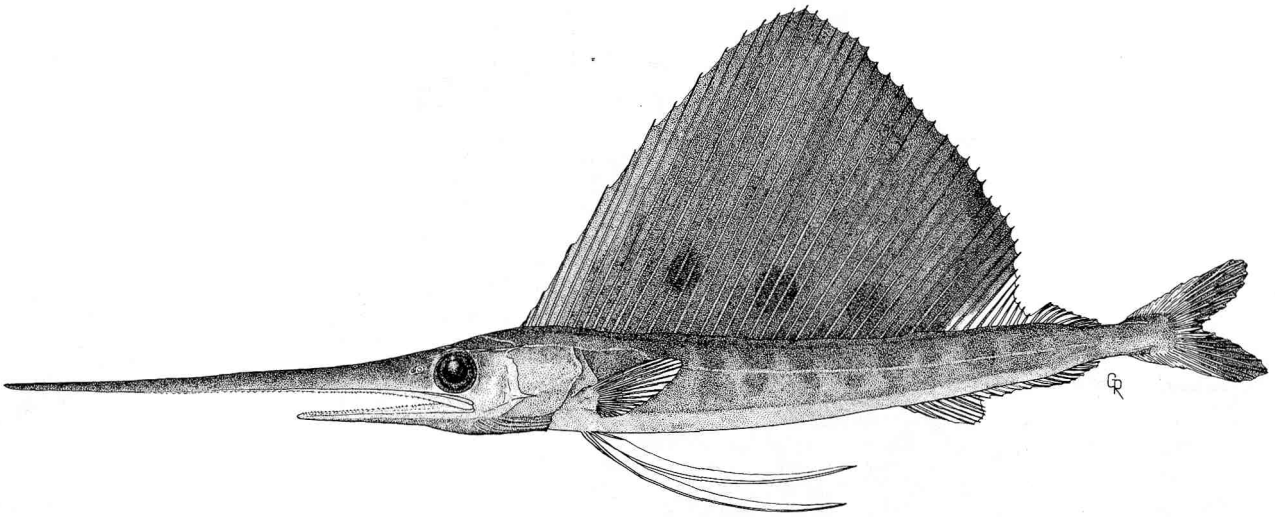

FIGURE 3.—Juvenile sailfish, 98.9 mm. standard length, *Silver Bay* Sta. 2201.

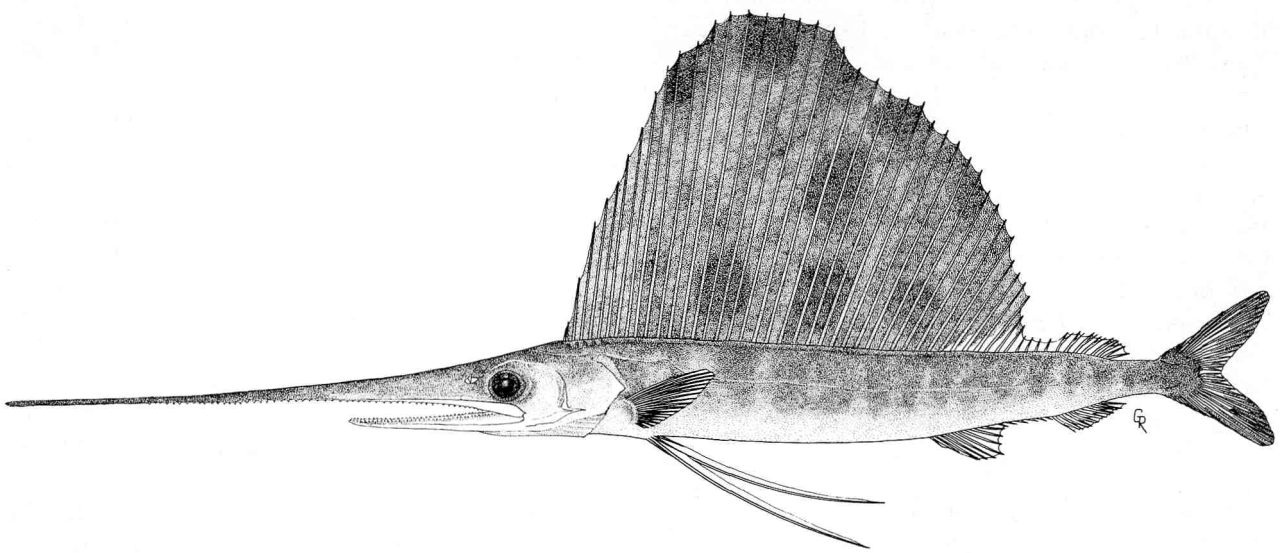

FIGURE 4.—Juvenile sailfish, 155 mm. standard length, *Silver Bay* Sta. 2139.

fish about 100 mm. SL have 7 to 12 bars, and the few specimens between 150 and 200 mm. SL have 12 to 14 bars. The largest western Atlantic specimen, 216 mm. SL, has 22 bars. Throughout the size range examined here the bars are distinct on some fish but indistinct on others and arranged in pairs on some specimens but not on others.

FIN RAYS

The numbers of fin rays for western and eastern Atlantic specimens with undamaged fins are within the adult complements. I prepared tables of numbers of fin rays for western Atlantic specimens only. The fins of a number of eastern Atlantic specimens were damaged, and too few counts are available to make useful tables. The numbers of fin rays for eastern Atlantic specimens are within the ranges for western Atlantic specimens, except for a few differences which are mentioned in the discussions.

The total number of dorsal fin rays ranges from 47 to 56 (mean, 51.6) for 142 western Atlantic

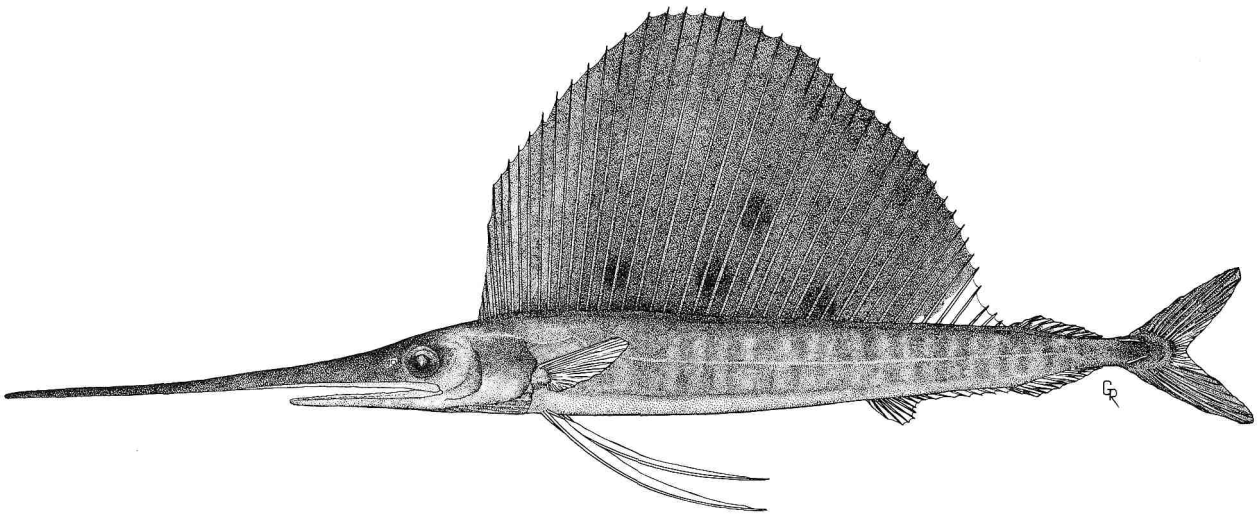

FIGURE 5.—Juvenile sailfish, 216 mm. standard length, *Silver Bay* Sta. 2172.

specimens[3] (one eastern Atlantic specimen has 57), and the total number of anal fin rays ranges from 21 to 25 (mean, 23.6) for 143 fish (one eastern Atlantic specimen has 20). Table 1 shows the total numbers of dorsal and anal fin rays for 139 western Atlantic sailfish.

Table 2 shows the numbers of rays in the anterior and posterior portions of the dorsal fin for 142 western sailfish. The range for the anterior portion is 43 to 50 (mean, 45.0) for 46 specimens (32.4 percent) with six rays in the posterior portion (51 for one eastern Atlantic specimen), and 40 to 49 (mean, 45.0) for 96 specimens (67.6 percent) with seven rays in the posterior portion. The mean of total number of rays in the dorsal fin is 51.0 for western Atlantic specimens with six rays in the posterior portion and 52.0 for those with seven rays in the posterior portion.

Table 3 shows the numbers of rays in the anterior and posterior portions of the anal fin for 143 western Atlantic sailfish. The range for the anterior portion is 15 to 19 (mean, 17.3) for 66 specimens (46.2 percent) with six rays in the posterior portion (14 for one eastern Atlantic specimen), and 14 to 18 (mean, 16.8) for 77 specimens (53.8 percent) with seven rays in the posterior portion. The mean of total number of rays in the anal fin is 23.3 for western Atlantic specimens with six rays in the posterior portion and 23.8 for those with seven rays in the posterior portion.

Table 4 shows the numbers of fin rays in the posterior portions of the dorsal and anal fins for the western Atlantic sailfish. Nearly half (46.8 percent) of 141 specimens have seven rays in this

[3] The numbers of fish shown in tables 1 to 4 are not the same. Of the 154 western Atlantic specimens, 139 had complete (undamaged) dorsal and anal fins, the rest had a complete dorsal or anal fin, or complete anterior or posterior portions of these fins. To take advantage of the greatest number of specimens for correlations, I used all sailfish with counts for desired fins or portions of fins. The same fish were not always involved.

TABLE 1.—*Number and (in parentheses) percentage of sailfish with different combinations of dorsal and anal fin rays, in a series of 139 specimens from the western Atlantic*

Anal fin rays	Dorsal fin rays									
	47	48	49	50	51	52	53	54	55	56
Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
21				1 (0.7)		1 (0.7)				
22			4 (2.9)	3 (2.2)	4 (2.9)	1 (0.7)				
23		1 (0.7)	7 (5.0)	9 (6.5)	9 (6.5)	10 (7.2)	8 (5.8)	3 (2.2)	1 (0.7)	
24	1 (0.7)		3 (2.2)	7 (5.0)	14 (10.1)	11 (7.9)	9 (6.5)	8 (5.8)	2 (1.4)	1 (0.7)
25			2 (1.4)	1 (0.7)	1 (0.7)	5 (3.6)	5 (3.6)	6 (4.3)		1 (0.7)

TABLE 2.—*Number and (in parentheses) percentage of sailfish with different combinations of fin rays in the anterior and posterior portions of the dorsal fin, in a series of 142 specimens from the western Atlantic*

Posterior portion fin rays	Anterior portion fin rays										
	40	41	42	43	44	45	46	47	48	49	50
Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
6	----------	----------	----------	10 (7.0)	9 (6.3)	11 (7.7)	10 (7.0)	2 (1.4)	3 (2.1)	----------	1 (0.7)
7	1 (0.7)	2 (1.4)	5 (3.5)	11 (7.7)	18 (12.7)	19 (13.4)	21 (14.8)	15 (10.6)	3 (2.1)	1 (0.7)	----------

TABLE 3.—*Number and (in parentheses) percentage of sailfish with different combinations of fin rays in the anterior and posterior portions of the anal fin, in a series of 143 specimens from the western Atlantic*

Posterior portion fin rays	Anterior portion fin rays					
	14	15	16	17	18	19
Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
6	----------	1 (0.7)	11 (7.7)	27 (18.9)	23 (16.1)	4 (2.8)
7	1 (0.7)	4 (2.8)	20 (14.0)	33 (23.1)	19 (13.3)	----------

portion of both fins, 24.8 percent have six rays in each, 20.6 percent have seven dorsal and six anal rays, and the rest (7.8 percent) have six dorsal and seven anal rays. Twenty (about 75 percent) of 27 eastern Atlantic specimens have six rays in both fins.

The number of pectoral fin rays ranges from 17 to 20; 10 (6.9 percent) of 145 western Atlantic specimens have 17, 126 (86.9 percent) have 18, 8 (5.5 percent) have 19, and 1 (0.7 percent) has 20. Fifteen of 28 eastern Atlantic specimens have 17 rays, 12 have 18, and 1 has 19.

All specimens have nine upper and eight lower principal caudal rays. Counts were 11 or 12 upper and lower secondary caudal rays for several specimens (40–216 mm. SL) which were cleared and stained or X-rayed.

TABLE 4.—*Number and (in parentheses) percentage of sailfish with different combinations of fin rays in the posterior portions of the dorsal and anal fins, in a series of 141 specimens from the western Atlantic*

Anal fin rays	Dorsal fin rays	
	6	7
Number	*Number*	*Number*
6	35 (24.8)	29 (20.6)
7	11 (7.8)	66 (46.8)

Fin-ray counts given by Robins and de Sylva (1963) for adult *Istiophorus platypterus* are: dorsal spines, 40 to 49; second dorsal rays, 6 to 8 (1 of 59 fish had 8 rays); anal spines, 12 to 17; second anal rays, 6 to 8 (1 of 59 fish had 8 rays), pectoral rays, 18 to 21. The difference between their range of 40 to 49 dorsal spines and my range of 43 to 50 rays in the anterior portion of the dorsal fin and their range of 12 to 17 anal spines and my range of 14 to 19 rays in the anterior portion of the anal fin may reflect degeneration of several rays immediately ahead of the second dorsal and anal fins and their overgrowth by skin in the adult. A comparison of the percentages of my fish with six and seven rays in the posterior portions of the dorsal and anal fins with the information given by Robins and de Sylva is interesting. Roughly, one-third of their and my (western Atlantic) fish (32.2 percent and 32.4 percent, respectively) had six second dorsal fin rays and two-thirds (66.1 percent and 67.6 percent, respectively) had seven second dorsal fin rays (they recorded one fish with eight second dorsal rays, I had none). They recorded these same percentages of sailfish for numbers of second anal rays; 32.2 percent with six, 66.1 percent with seven, and one with eight rays. My counts are different; they show 46.2 percent with six rays, 53.8 percent with seven, and none with 8 in the posterior portion of the anal fin.

REGRESSIONS OF BODY PARTS ON TRUNK LENGTH

Comparisons of the changes in various body parts of fishes during development have been variously based on standard, fork, or total length. The snout and caudal rays are so frequently damaged in the billfishes that measurements involving one or both of these parts may be inaccurate. Body length, recommended by Rivas (1956) as the preferred base length for billfishes, is the distance between the tip of the mandible and the

tips of the middle caudal fin rays. This measurement involves fin rays that are fragile and frequently damaged on small specimens. The base length that I selected for my comparisons is the trunk length, defined by de Sylva (1957) as the distance between the posterior margin of the orbit and the anterior insertion of the caudal keels. This length involves neither the snout nor the caudal rays.[4]

[4] See definition for trunk length in section on methods and data for determination of posterior point for this measurement of sailfish without caudal keels.

Initially, individual measurements of selected body parts of the western Atlantic sailfish were plotted against trunk length on arithmetic paper (figs. 6–12). The distribution of the data suggested that the relatively fewer specimens with trunk length greater than 60 mm. should be treated separately. Two regression lines were calculated—one for those with trunk length less than 62 mm. and one for longer specimens. The regression equation is $Y=a+bX$ (table 5). Inspection of the graphs with the calculated regression lines added suggests that the location of point of inflection varies some-

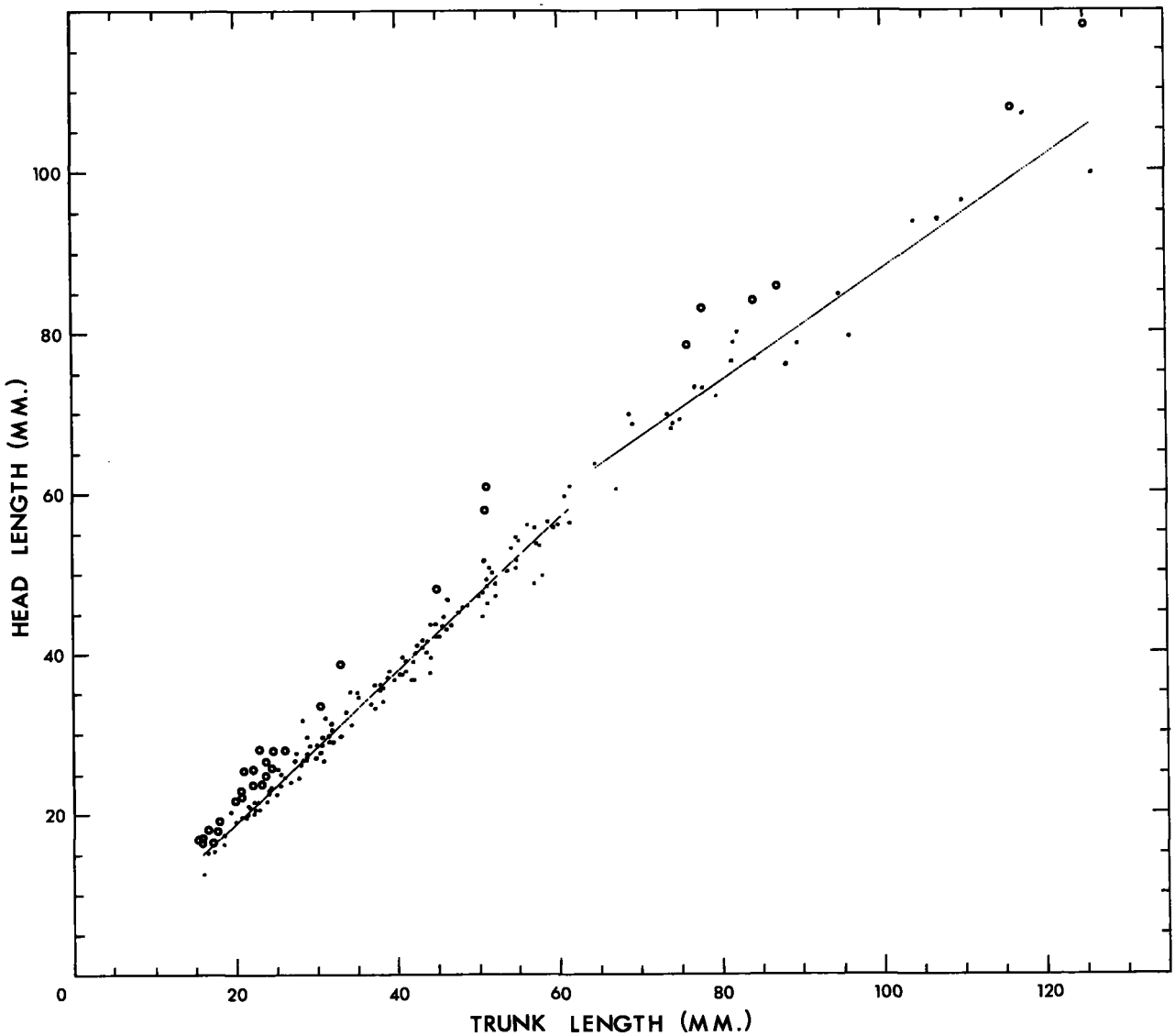

FIGURE 6.—Relation of head length to trunk length in sailfish. Small dots represent western Atlantic specimens; open circles, eastern Atlantic specimens. Regression lines represent western Atlantic data only.

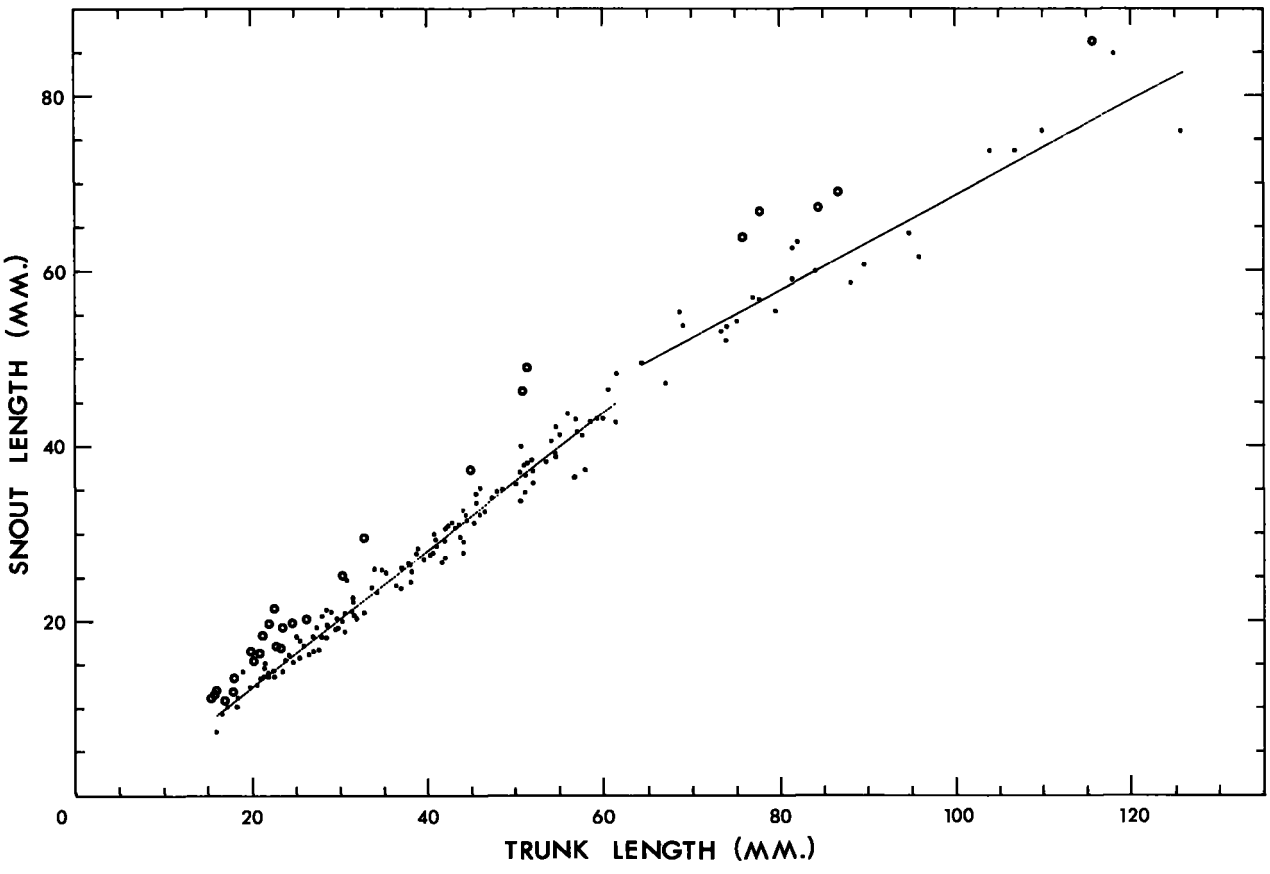

FIGURE 7.—Relation of snout length to trunk length in sailfish. Small dots represent western Atlantic specimens; open circles, eastern Atlantic specimens. Regression lines represent western Atlantic data only.

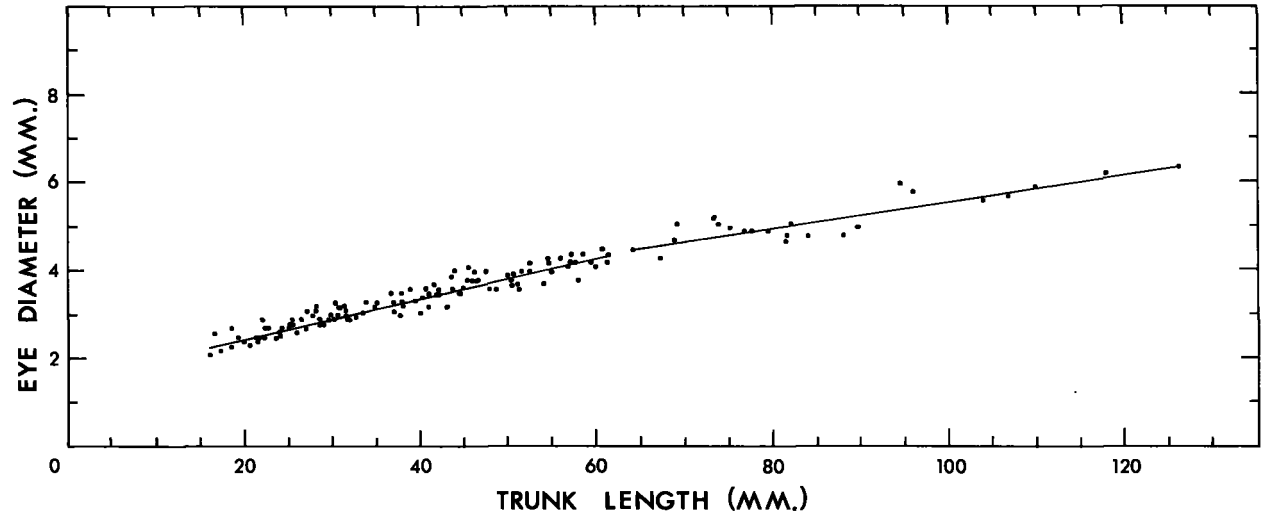

FIGURE 8.—Relation of eye diameter to trunk length in sailfish from the western Atlantic.

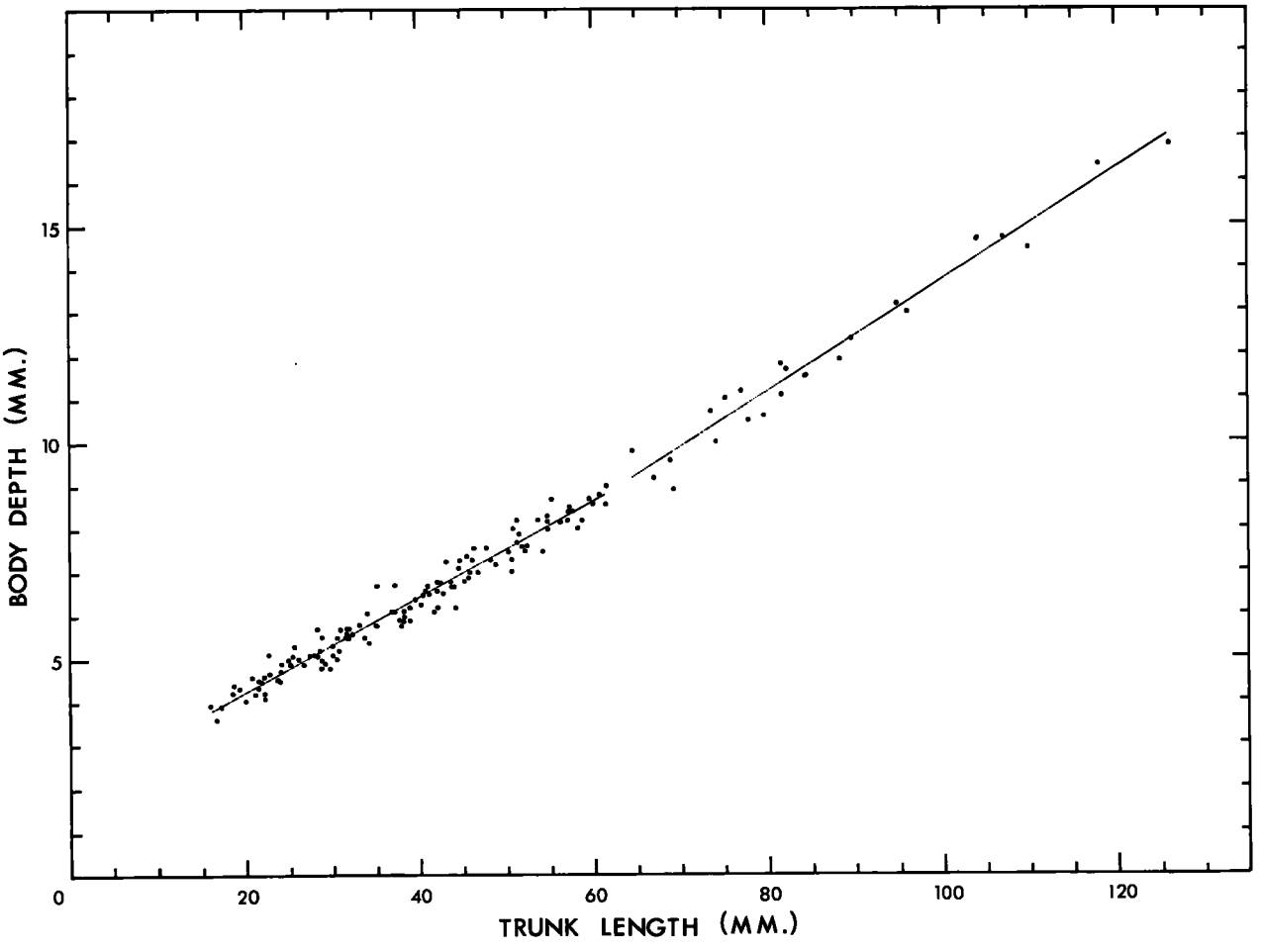

FIGURE 9.—Relation of body depth to trunk length in sailfish from the western Atlantic.

TABLE 5.—*Statistics describing regressions of body parts on trunk length, or body length, for sailfish from the western Atlantic*

[$\bar{x}$, mean of values of X; $\bar{y}$, mean of values of Y; N, number of specimens; b, slope of regression line; a, Y-intercept of regression line; Sy.x, standard deviation from regression (standard error of estimate)]

Independent variable X and specimen size [1]	Dependent variable Y	$\bar{x}$	$\bar{y}$	N	b	a	Sy.x
Trunk length:							
Small	Head length	37.92	35.87	130	0.942	0.142	1.610
Large	do	86.04	78.32	24	.694	18.592	3.263
Small	Snout length	37.92	26.37	130	.782	−3.279	1.517
Large	do	86.04	60.94	24	.538	14.619	3.209
Small	Eye diameter	37.65	3.30	121	.045	1.626	.111
Large	do	86.56	5.19	23	.029	2.677	.273
Small	Body depth	37.92	6.20	130	.109	2.067	.273
Large	do	86.04	11.92	24	.127	.997	.367
Small	Pectoral fin length	37.92	5.82	127	.109	1.678	.372
Large	do	83.85	9.99	18	.078	3.421	.444
Small	Pelvic fin length	37.26	15.04	124	.405	−.042	.937
Large	do	83.85	33.40	18	.348	4.237	1.499
Small	Pelvic fin-anal fin	37.92	18.64	130	.486	.227	.510
Large	do	86.04	41.32	24	.477	.282	.923
Body length:							
Small	Trunk length	52.87	37.58	124	.786	−3.961	.981
Large	do	114.38	85.79	22	.796	−5.204	1.377

[1] Small, 16.0–61.5 mm. trunk length; large, 64.5–126 mm. trunk length.

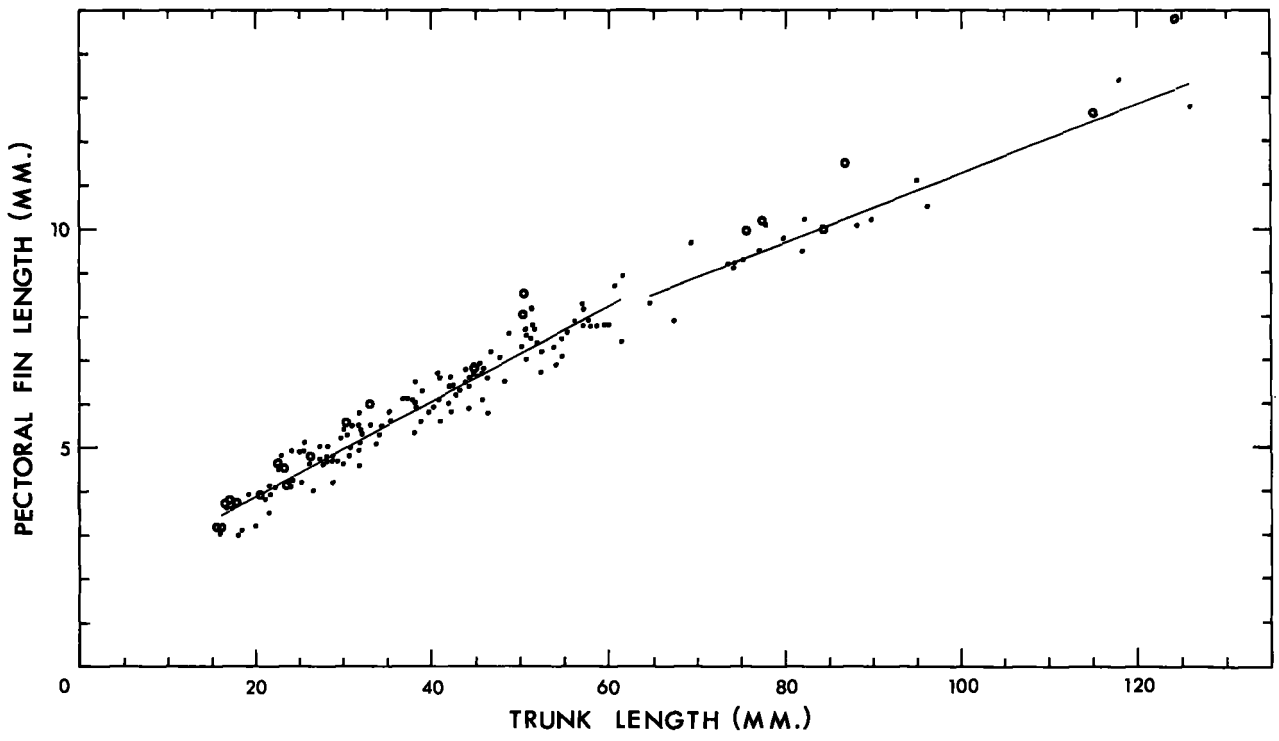

FIGURE 10.—Relation of pectoral fin length to trunk length in sailfish. Small dots represent western Atlantic specimens; open circles, eastern Atlantic specimens. Regression lines represent western Atlantic specimens only.

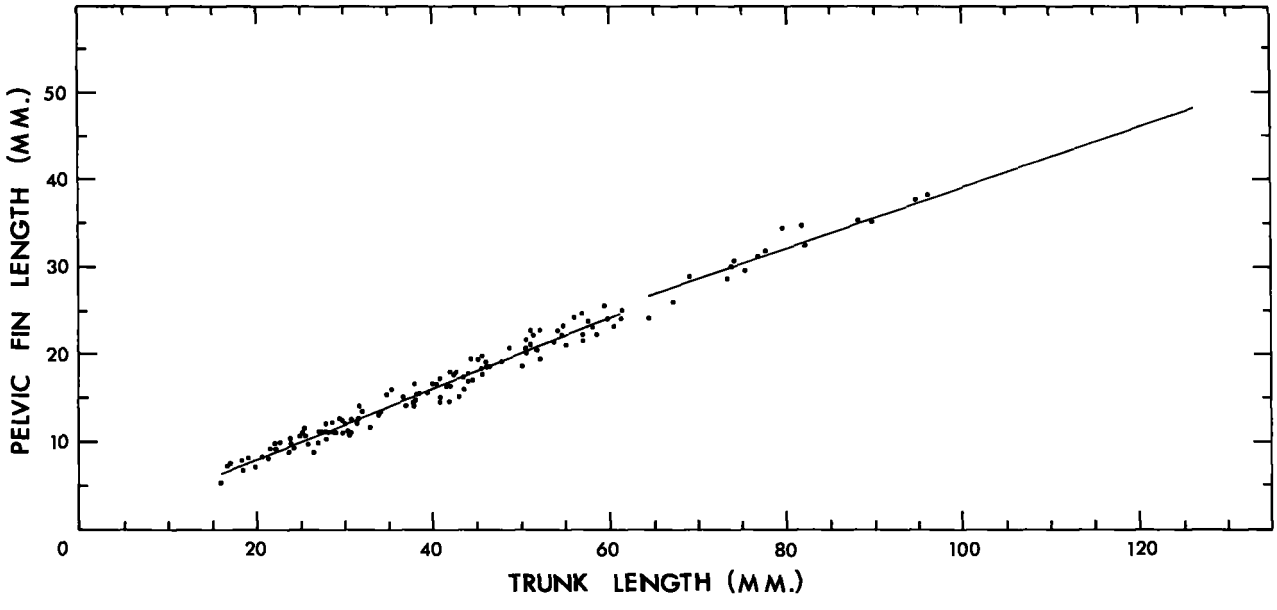

FIGURE 11.—Relation of pelvic fin length to trunk length in sailfish from the western Atlantic.

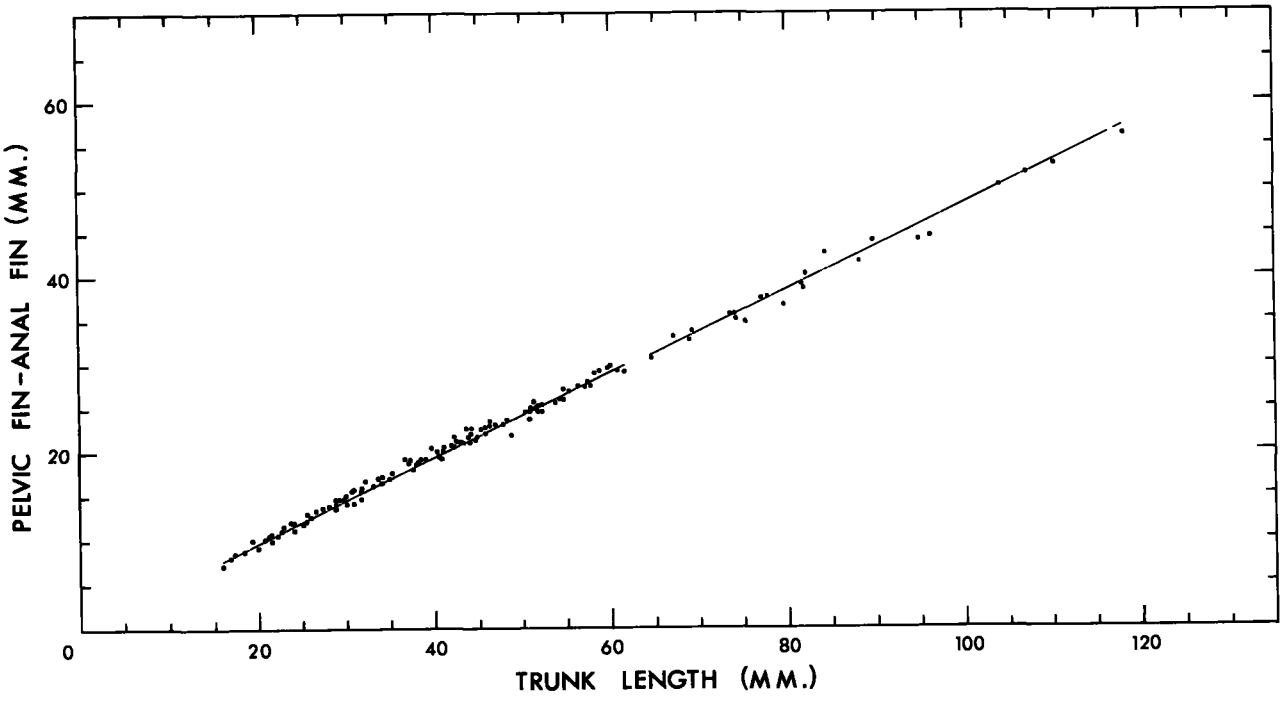

FIGURE 12.—Relation of the distance pelvic fin-anal fin to trunk length in sailfish from the western Atlantic.

what with body part and that some parts have little or no inflection. Figure 13, which illustrates the regression of trunk length on body length, is included to show that this relation is rectilinear throughout the size range; the calculated regression line for specimens with trunk length greater than 62 mm. has the same slope (b) and is merely an extension of that for smaller fish.

Subsequent to preparation of plots of data and calculation of regression lines for western Atlantic sailfish, I obtained measurements from 34 eastern Atlantic fish and plotted them on graphs. The data from the eastern Atlantic are too meager, however, for making calculations of regressions—the number of specimens is too small and the size distribution is poor. Because the greater numbers of western Atlantic specimens might possibly hide differences between the two groups if the data were combined, I plotted them separately on the same graph, distinguishing the two groups. I shall limit my comments to differences this simple comparison suggests.

The individual plots of data for eastern Atlantic sailfish generally lie within the ranges for fish from the western Atlantic for eye diameter, body depth, pelvic fin length, and distance from pelvic fin to anal fin; these data are, therefore, not shown on the figures showing these relations (figs. 8, 9, 11, and 12, respectively). Measurements of snout length, head length, and pectoral fin length, however, generally lie higher on the graphs for fish from the eastern Atlantic than for those from the western Atlantic (figs. 6, 7, and 10). The longer head (fig. 6) is attributable to the generally longer snout (fig. 7). The pectoral fin is also generally longer in eastern Atlantic sailfish (fig. 10).

ACKNOWLEDGMENTS

Staff members of BCF Biological Laboratory, Brunswick, Ga., helped collect western Atlantic specimens, made X-ray photographs, and cleared and stained study material; they also prepared illustrations and reviewed the manuscript. Personnel of BCF Exploratory Fishing and Gear Research Station, Brunswick, Ga., also helped collect western Atlantic specimens. George C. Miller, of BCF Tropical Atlantic Biological Laboratory, Miami, Fla., made available eastern Atlantic specimens collected off west Africa. Grady W. Reinert prepared illustrations, and Elbert H. Ahlstrom, Donald P. de Sylva, and R. Michael Laurs reviewed the manuscript.

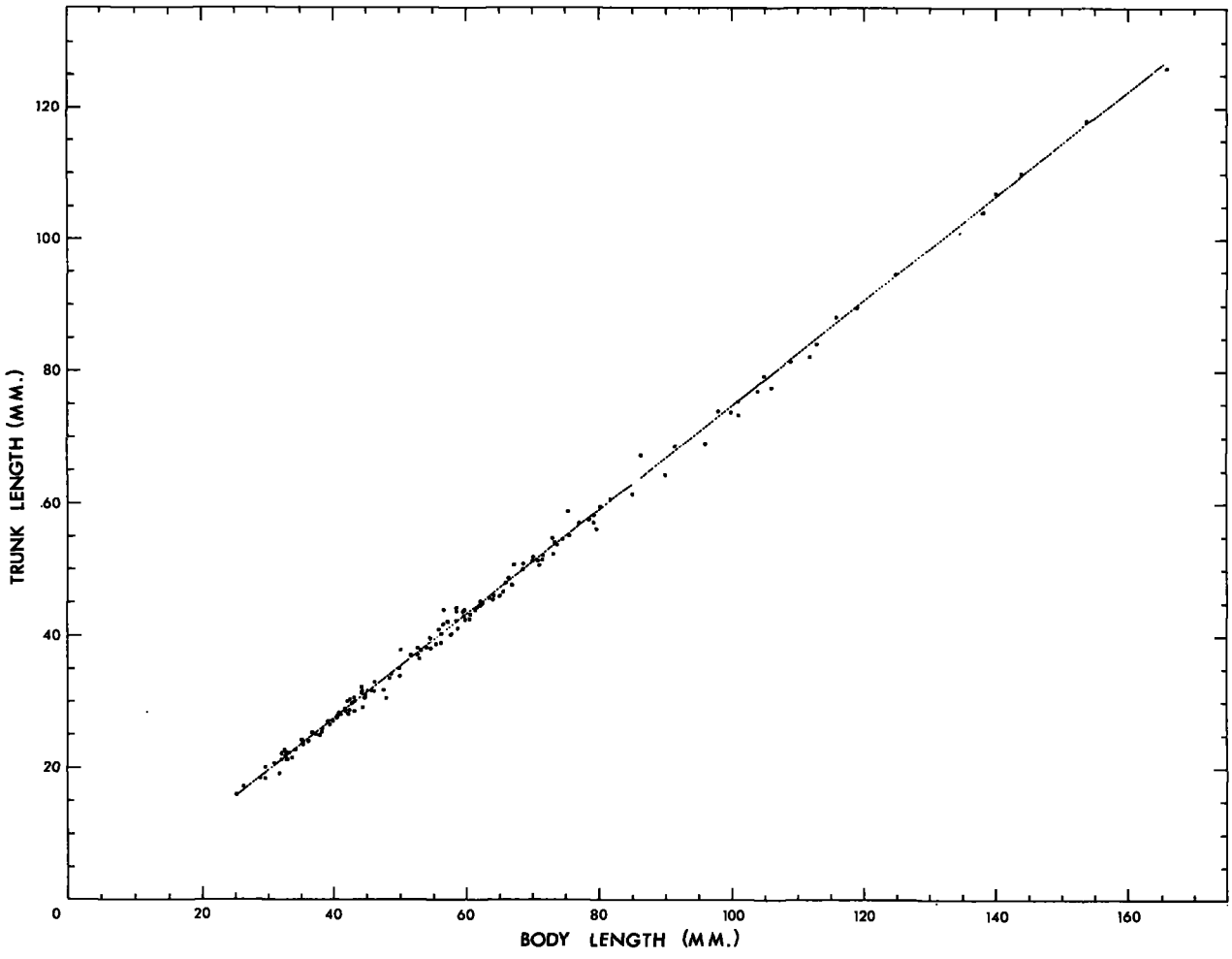

FIGURE 13.—Relation of trunk length to body length in sailfish from the western Atlantic.

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MOLLUSKS AND BENTHIC ENVIRONMENTS IN HILLSBOROUGH BAY, FLORIDA[1]

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ABSTRACT

Analysis of benthic mollusks and sediments at 45 stations showed that the diversity and abundance of mollusks was affected by bottom conditions which were influenced in varying degrees by domestic and industrial pollution and dredging. Nineteen stations had no living mollusks, 18 stations had one or more of the four mollusk species that were predominant, and 8 stations had mollusks well represented by numerous species and large numbers of individuals. Stations with no living mollusks were termed unhealthy, and others were designated marginal or healthy on the basis of the mollusks present. From station data, isopleths connecting similar areas indicated that 42 percent of the bay bottom was unhealthy, 36 percent marginal, and 22 percent healthy. Infrequent occurrence of the American oyster (*Crassostrea virginica*) further suggests that the major portion of Hillsborough Bay was seriously contaminated. An appendix has a checklist of the 64 species of mollusks collected in the bay.

This report treats the relation of diversity and abundance of mollusks to bottom conditions in Hillsborough Bay, Fla., where dredging and pollution from domestic and industrial sources now control the ecology. The data are from benthic and hydrological surveys by the Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla., during August and September 1963.

The problem of pollution in coastal waters has stimulated research to establish environmental quality criteria based on physical, chemical, and biological components of marine and brackish water communities. Mollusks are useful in such studies because the group is well described taxonomically and contains species that vary greatly in habitat selection, mode of feeding, and tolerance to environmental change. Furthermore, most mollusks are sedentary as adults and the remains of their shells provide a semipermanent record of their occupancy.

The ecology of mollusks in natural waters has been studied by a number of authors. Previous studies on the ecology of mollusks in natural and polluted waters of the southeastern United States provided a basis for the interpretation of collections from Hillsborough Bay. Reports on mollusk assemblages in unpolluted estuaries included work by Ladd (1953), Parker (1960), and Brett (1963). Within the same geographic area, studies of mollusks in polluted estuaries include work on the ecological effects of petroleum wastes (Mackin and Hopkins, 1961), pesticides (Butler, 1966), siltation and dredging (Mackin, 1961), channelization (Chambers and Sparks, 1959), and domestic sewage (McNulty, 1966). The work by McNulty, and an earlier series of studies with collaborators, represent a comprehensive study over a period of 11 years in Biscayne Bay, Fla., before and after pollution abatement.

ECOLOGICAL FEATURES OF HILLSBOROUGH BAY

Hillsborough Bay lies in the upper part of Tampa Bay, east of Interbay Peninsula and north of a line between Gadsden Point and Newman Branch (fig. 1). The 56-km. shoreline encompasses a water area of about 10,360 ha. Forty percent of this area is 1.8 m. or less, and except for dredged ship channels up to 10.5 m. deep, the greatest depth in the bay is about 5.4 m. Tidal range is normally 0.9 m. or less, and maximum tidal current is under 51 cm./second (1 knot)—see Olson and Morrill (1955) and Taylor and Saloman (1969). Portions of the bay around Davis Island, Seddon Island, McKay Bay, and Port Sutton have been dredged for fill material or deepened for shipping (fig. 1). Other dredging in the bay centers around oyster shell deposits which are used for the construction industry (Dawson, 1953). These deposits are extensive and show that the American oyster, *Crassostrea virginica*, once

[1] Contribution No. 56, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla. 33706.

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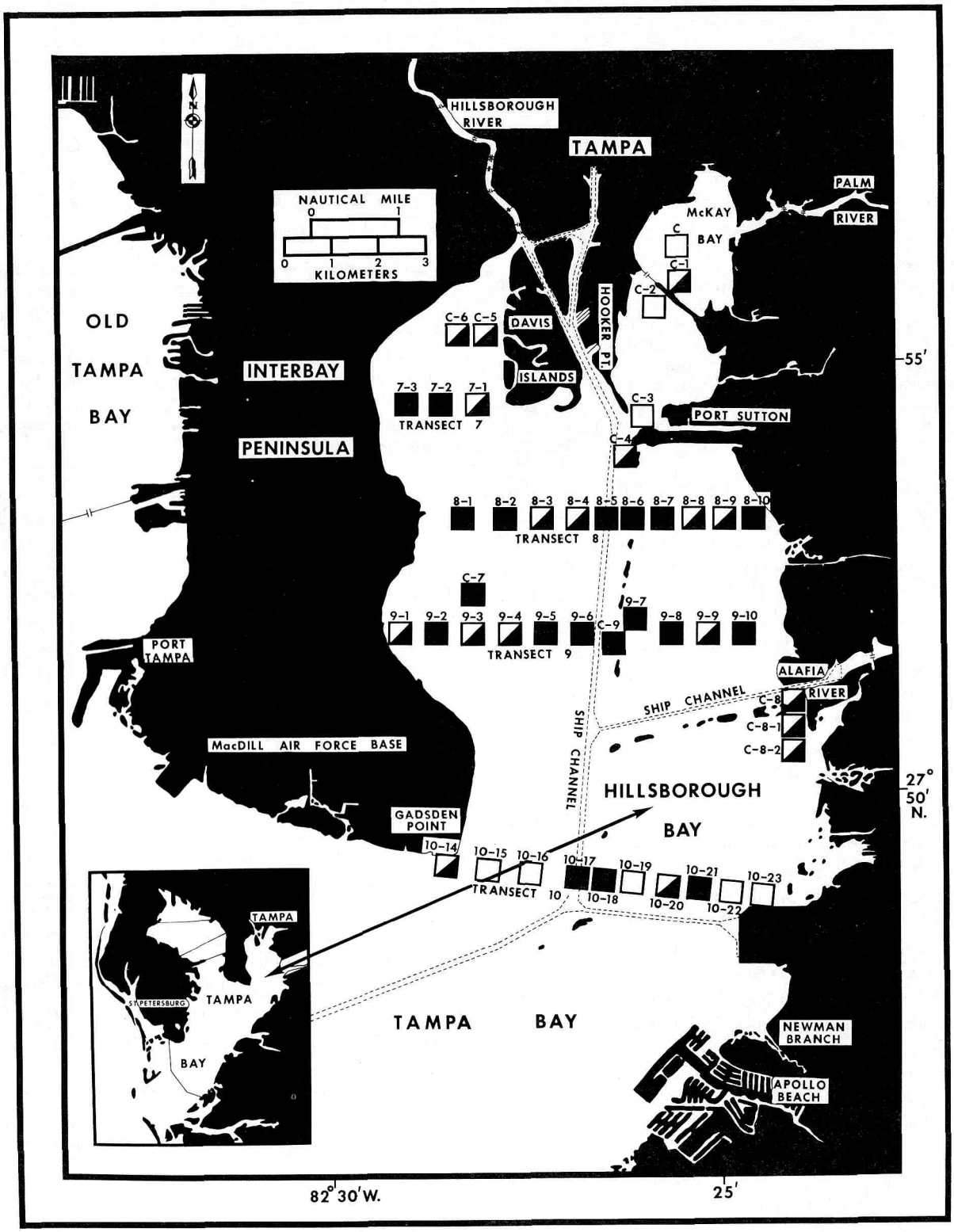

FIGURE 1.—Tampa Bay and Hillsborough Bay showing channels, survey transects, collecting stations, and environmental conditions at each station—healthy stations (unshaded); marginal stations (half-shaded); unhealthy stations (shaded)—August and September 1963.

flourished in Hillsborough Bay as it does today along most of the Gulf Coast between Cape Sable and the Rio Grande (Butler, 1954). The annual mean and range of salinity (22.20 and 12.65–27.84 p.p.t.), water temperature (24.96° and 11.65°–34.00° C.), and other hydrological features of the bay have been reported by Saloman and Taylor (1968).

In addition to considerable physical alteration of the bay, water chemistry and resident biota have changed decidedly as a result of domestic and industrial sewage. The principal identified pollutants are compounds of phosphorus and nitrogen, and highly organic suspended solids. Regional sanitation plants provide only primary sewage treatment for 120,000 m.[3]/day (30 m.g.d.—million gallons per day) and serve a population of about 300,000. The treated effluent carries more than 50 percent of the suspended solids present before treatment and adds an enormous load of phosphorus and nitrogen.[2] The solids are deposited as sludge, and phosphorus and nitrogen are available as nutrients for plants and animals. The phosphate industry provides additional sediment and phosphorus, and natural land drainage provides substantial amounts of phosphorus, nitrogen, iron, copper, and organic compounds (Odum, 1953; Dragovich and May, 1962; Dragovich, Kelly, and Goodell, 1968). Dragovich et al. (1968) estimated that the Hillsborough and Alafia Rivers together add 557 metric tons of phosphorus to the bay each year. In the bay the annual mean concentration of total phosphorus is 19.38 μg.at./liter, and the total nitrogen (Kjeldahl) is 80.17 μg.at./liter. Comparative figures for Tampa Bay entrance (P=14.39; N=45.08 μg.at./liter) and the nearshore Gulf of Mexico (P=3.6; N=23.4 μg.at./liter) give some idea of the extraordinary mineral enrichment that exists in Hillsborough Bay (Saloman and Taylor, 1968). In Biscayne Bay, Fla., McNulty, Reynolds, and Miller (1959) and McNulty (1966) found that domestic sewage adversely affected the biotic environment. There, daily discharge of 120,000 to 200,000 m.[3]/day (30-50 m.g.d.) of raw sewage raised the average concentration of total phosphorus to 3 μg.at./liter or about one-sixth of the concentration now in Hillsborough Bay.

Enrichment of Hillsborough Bay by phosphorus and nitrogen causes excessive growth of phytoplankton and filamentous algae (Dragovich, Kelly, and Kelly, 1965). The heavy growth of algae and the phytoplankton blooms cause marked fluctuations in dissolved oxygen. In periods of photosynthetic activity, oxygen concentrations have exceeded 8 ml./liter but at other times, BOD (biochemical oxygen demand) may reduce dissolved oxygen to 1 ml./liter or less at the bottom (Saloman, Finucane, and Kelly, 1964; Saloman and Taylor, 1968; FWPCA, personal communication[3]).

Other consequences of pollution in Hillsborough Bay include high water turbidity (annual average, 19.19 Jackson Turbidity Units), low light transmission (annual average, 30.3 percent of incident radiation at 60 cm. below the water surface), and very little growth of marine grasses (Taylor and Saloman, 1966; Saloman and Taylor, 1968; and Taylor and Saloman, 1969). In their comparative study of macrofauna in major geographic areas of Tampa Bay, Sykes and Finucane (1966) provided further biological evidence of pollution in the bay. From quantitative sampling, their work showed that catches of fish and crustaceans were lower in Hillsborough Bay than in any other region of the estuary. The greatest catches came from Old Tampa Bay where environmental conditions differ from those in Hillsborough Bay mainly in terms of fewer and smaller sources of pollution, lower turbidity, lower nitrogen concentration, higher dissolved oxygen at the bottom, more sandy sediments, a more natural shoreline, and extensive beds of sea grasses.

PROCEDURES

We sampled mollusks together with bottom vegetation and sediments with a bucket dredge and rigid-frame net at 45 stations between August 13 and September 5, 1963 (fig. 1). The dredge dug 5 cm. into the bottom and had a capacity of 15 liters. It filled with sediment after covering an area of about 30 by 100 cm. The net skimmed the bottom and had an opening of 30.5 by 91.4 cm. It was hung with square-mesh netting with openings of 3.2 mm. (Taylor, 1965). At intertidal stations, the bottom was sampled by shovel and the

[2] Hillsborough County Health Department, Tampa, Fla. 33601, personal communication, 1969.

[3] Federal Water Pollution Control Administration, Tampa-Hillsborough Bay Project, Tampa, Fla. 33605, 1968.

net was pulled by hand. One dredge haul, or a nearly equivalent volume of sediment collected by shovel, and one 2-minute net haul were taken at each station. We collected water samples at each station with a Van Dorn bottle for determination of temperature, salinity, and pH. Water depth was measured by handline.

We removed the mollusks from bottom samples by sieving sediment and bottom debris on a screen of 0.701-mm. mesh (Tyler #24 screen[4]). Before sieving, we removed a subsample of sediment (about 300 cc.) from each bottom sample for analysis at the Sedimentological Laboratory, Florida State University. Their analyses included measurements of grain size, calcium carbonate, organic nitrogen, and organic carbon as well as statistical characteristics of mean grain size, sorting (as standard deviation), skewness, and kurtosis (Taylor and Saloman, 1969).

[4] References to trade names in this publication do not imply endorsement of commercial products.

DIVERSITY AND ABUNDANCE OF MOLLUSKS

We collected and identified 64 species of mollusks from bottom samples taken in Hillsborough Bay (Appendix). Of these species only 36 were represented by living individuals; furthermore, live mollusks were collected at only 26 of the 45 stations sampled. Samples at all stations where live mollusks were collected always included one or more of four species, i.e.: dwarf surf clam (*Mulinia lateralis*), paper mussel (*Amygdalum papyria*), common eastern nassa (*Nassarius vibex*), and stout tagelus (*Tagelus plebeius*). On an individual basis, *M. lateralis* was present in 65 percent of the station samples that contained live mollusks; the incidences of *A. papyria*, *N. vibex*, and *T. plebeius* were 58, 54, and 35 percent, respectively (table 1). The next most numerous mollusks were the crown conch (*Melongena corona*) and the lunar dove-shell (*Mitrella lunata*) which occurred at 6 of the 26 stations where live mollusks were found.

TABLE 1.—*Numbers of living mollusks by species and station collected from Hillsborough Bay, Fla., August and September 1963*

[Number of times a station sampled in parentheses]

Species	Station numbers																
	7-1 (2)	7-2 (2)	7-3 (2)	8-1 (2)	8-2 (2)	8-3 (2)	8-4 (2)	8-5 (2)	8-6 (1)	8-7 (2)	8-8 (2)	8-9 (2)	8-10 (2)	9-1 (1)	9-2 (2)	9-3 (2)	9-4 (2)	9-5 (2)
Mulinia lateralis						1	2				4	2				800	1	
Amygdalum papyria												40				1		
Nassarius vibex	4															122	4	
Tagelus plebeius												7		1				
Melongena corona						1												
Mitrella lunata																1		
Tellina versicolor																		
Ensis minor																		
Mercenaria campechiensis																	1	
Macoma tenta																		
Crepidula plana																		
Bittium varium																		
Thracia sp.																1		
Modiolus americanus												5						
Anadara transversa																		
Crassostrea virginica																		
Retusa canaliculata																		
Polinices duplicatus																		
Odostomia acutidens																		
Mystella planulata												5						
Epitonium humphreysi																		
Corbula caribaea																		
Anachis obesa																		
Tagelus divisus																		
Urosalpinx tampaensis																		
Nucula proxima																		
Natica pusilla																		
Laevicarium mortoni																		
Haminoea succinea																		
Epitonium angulatum																		
Crepidula fornicata																		
Corbula barrattiana																		
Brachidontes exustus																		
Polymesoda caroliniana																		
Acteon punctostriatus											4							
Ischnochiton papillosus						1												
Total number species	1	0	0	0	0	3	1	0	0	0	2	5	0	1	0	5	3	0
Total number individuals	4	0	0	0	0	3	2	0	0	0	8	59	0	1	0	925	6	0

TABLE 1.—*Numbers of living mollusks by species and station collected from Hillsborough Bay, Fla., August and September 1963*—Continued

[Number of times a station sampled in parentheses]

Species	Station numbers														
	9-6 (2)	9-7 (2)	9-8 (2)	9-9 (2)	9-10 (2)	10-14 (3)	10-15 (2)	10-16 (2)	10-17 (2)	10-18 (1)	10-19 (2)	10-20 (2)	10-21 (2)	10-22 (2)	10-23 (2)
Mulinia lateralis				4		21	63				10	1		35	
Amygdalum papyria						21	3				3	4		41	300
Nassarius vibex						9	10	3				1		4	5
Tagelus plebeius						12									
Melongena corona							1								
Mitrella lunata						203	359	1							30
Tellina versicolor							16	4			1			2	
Ensis minor						7								1	2
Mercenaria campechiensis								4			2			1	
Macoma tenta							7	4			2			1	
Crepidula plana						3		1							1
Bittium varium						10	1								10
Thracia sp.							2	1			1				
Modiolus americanus															
Anadara transversa							10				5				
Crassostrea virginica							3								
Retusa canaliculata							2								1
Polinices duplicatus														1	1
Odostomia acutidens							1								2
Mysella planulata															
Epitonium humphreysi							6							1	
Corbula caribaea								5			41				
Anachis obesa							22							1	
Tagelus divisus															
Urosalpinx tampaensis															
Nucula proxima											1				
Natica pusilla											2				
Laevicarium mortoni							3								
Haminoea succinea															
Epitonium angulatum							3								
Crepidula fornicata											1				
Corbula barratiana											2				
Brachidontes exustus															1
Polymesoda caroliniana															
Acteon punctostriatus															
Ischnochiton papillosus															
Total number species	0	0	0	1	0	8	17	8	0	0	12	3	0	10	10
Total number individuals	0	0	0	4	0	286	512	23	0	0	71	6	0	88	353

Species	Station numbers												Stations where collected	
	C (2)	C-1 (1)	C-2 (2)	C-3 (2)	C-4 (1)	C-5 (2)	C-6 (2)	C-7 (1)	C-8 (1)	C-8-1 (1)	C-8-2 (1)	C-9 (1)	Stations	Percentage of stations
													Number	*Percent*
Mulinia lateralis	129		268	99		8	150						17	65
Amygdalum papyria	26	1	16	80	2	3	22						15	58
Nassarius vibex		22	2	2		1	15						14	54
Tagelus plebeius	1		16	2					71	142	89		9	35
Melongena corona	10	1	4	5									6	23
Mitrella lunata			8										6	23
Tellina versicolor			8										5	19
Ensis minor				5		1							5	19
Mercenaria campechiensis													4	15
Macoma tenta													4	15
Crepidula plana	6												4	15
Bittium varium	17												4	15
Thracia sp.													4	15
Modiolus americanus	1			17			15						4	15
Anadara transversa			3										3	12
Crassostrea virginica			2	2									3	12
Retusa canaliculata													2	8
Polinices duplicatus													2	8
Odostomia acutidens													2	8
Mysella planulata	1												2	8
Epitonium humphreysi													2	8
Corbula caribaea													2	8
Anachis obesa				1									2	8
Tagelus divisus													1	4
Urosalpinx tampaensis			1										1	4
Nucula proxima													1	4
Natica pusilla													1	4
Laevicardium mortoni													1	4
Haminoea succinea	1												1	4
Epitonium angulatum													1	4
Crepidula fornicata													1	4
Corbula barratiana													1	4
Brachidontes exustus													1	4
Polymesoda caroliniana		1											1	4
Acteon punctostriatus													1	4
Ischnochiton papillosus													1	4
Total number species	9	4	10	9	1	4	4	0	1	1	1	0		
Total number individuals	192	25	328	159	2	13	202	0	71	142	89	0		

Live specimens of *M. lateralis*, *A. papyria*, *N. vibex*, and *T. plebeius* indicated bottom conditions by their presence or absence and by their abundance in relation to other live mollusks. On the basis of the occurrence and distribution of these four species, bottom environments were classified as healthy or marginal. Healthy stations were those where indicator species were less than 50 percent of all live mollusk species present; at marginal stations, the indicators represented 50 percent or more of all live species present. Unhealthy stations were those where no living mollusks were collected (fig. 1 and tables 2–4). The number of living mollusks was generally higher at healthy than at marginal stations except at marginal station 9–3 where *M. lateralis* and *N. vibex* were unusually abundant. Furthermore, on the basis of station classification the entire area of the bay was divisible into healthy, marginal, and unhealthy zones.

The four species selected as indicators for the bay, and perhaps the crown conch as well, may be useful for biological evaluation of the environment in estuarine water of the southeastern and Gulf States. Table 5 represents a summary of ecological literature and shows the extreme ranges of environmental conditions that these five mollusks can tolerate under natural conditions.

HEALTHY STATIONS

Eight stations, or about 18 percent of those having live mollusks, were classified as healthy. The average incidence of indicator species at these stations was 27 percent, and the average numbers per station were 11 species and 225 individuals (table 2).

TABLE 2.—*Biotic and physical characteristics of healthy benthic stations in Hillsborough Bay, Fla., August and September 1963*

Station	Species [1]	Individual [1]	Indicator species [1]	Depth	Mean sediment grain size	Sediment sorting	Sediment type	Bottom vegetation	Bottom salinity
	Number	*Number*	*Percent*	*M.*	*ø*	*ø*			*P.p.t.*
C	9	192	33	1.7	4.05	2.5	Coarse silt	*Gracilaria* sp.	18.19
C-2	10	328	40	4.7	2.28	1.0	Fine sand	*Gracilaria* sp.	18.56
C-3	9	213	44	2.0	2.78	1.6	Fine sand	*Gracilaria* sp.	16.35
10-15	17	512	18	3.0	2.74	1.4	Fine sand	*Gracilaria* sp.	21.82
10-16	8	23	13	6.0	3.15	1.5	Very fine sand	None	22.62
10-19	12	71	17	3.7	2.02	1.8	Fine sand	None	22.95
10-22	10	88	33	2.0	2.84	1.3	Fine sand	*Gracilaria* sp.	22.43
10-23	10	353	20	1.0	2.59	.8	Fine sand	*Gracilaria* sp.	21.26
Mean	11	225	27	3.0	2.80	1.5	Fine sand		20.52
Range			13–44	1.0–6.0	2.02–4.05	.8–2.5			18.19–22.95

[1] Collected alive.

TABLE 3.—*Biotic and physical characteristics of marginal benthic stations in Hillsborough Bay, Fla., August and September 1963*

Station	Species [1]	Individual [1]	Indicator species [1]	Depth	Mean sediment grain size	Sediment sorting	Sediment type	Bottom vegetation	Bottom salinity
	Number	*Number*	*Percent*	*M.*	*ø*	*ø*			*P.p.t.*
C-1	4	25	50	1.0	2.32	1.8	Fine sand	None	18.33
C-4	1	2	100	1.0	2.95	1.2	Fine sand	None	15.59
C-5	4	13	75	4.2	2.58	1.0	Fine sand	None	19.78
C-6	4	202	75	2.0	2.88	1.0	Fine sand	None	18.96
C-8	1	71	100	.7	2.51	1.1	Fine sand	None	.74
C-8-1	1	142	100	.7	2.95	1.6	Fine sand	None	1.15
C-8-2	1	89	100	.3	5.28	2.6	Medium silt	None	3.69
7-1	1	4	100	2.0	3.04	1.1	Very fine sand	None	17.79
8-3	3	13	50	3.6	4.09	2.2	Coarse silt	None	19.78
8-4	1	2	100	3.9	5.23	2.7	Medium silt	None	20.50
8-8	2	8	50	2.8	3.14	1.4	Very fine sand	None	16.56
8-9	5	57	60	1.0	2.51	.5	Fine sand	None	18.78
9-1	1	1	100	.3	2.53	.7	Fine sand	None	17.25
9-3	5	925	60	2.0	2.38	.8	Fine sand	None	18.37
9-4	3	6	67	2.4	2.25	.7	Fine sand	None	18.51
9-9	1	4	100	2.8	3.37	1.8	Very fine sand	None	17.70
10-14	8	267	50	1.0	2.68	.8	Fine sand	*Gracilaria* sp.	20.61
10-20	3	6	100	3.9	2.88	1.6	Fine sand	None	22.92
Mean	3	102	80	1.9	3.09	1.4	Very fine sand		15.90
Range			50–100	.3–4.2	2.25–5.28	.5–2.7			.74–22.92

[1] Collected alive.

TABLE 4.—*Biotic and physical characteristics of unhealthy benthic stations in Hillsborough Bay, Fla., August and September 1963*

Station	Depth	Mean sediment grain size	Sediment sorting	Sediment type	Bottom vegetation	Bottom salinity
	M.	Ø	Ø			*P.p.t.*
C–7	0.7	−0.95	1.4	Very coarse sand	None	18.33
C–9	.7	−.77	2.1	Very coarse sand	None	16.22
7–2	4.2	5.76	2.3	Medium silt	*Gracilaria* sp.	17.79
7–3	2.7				None	17.61
8–1	3.9	5.65	2.5	Medium silt	None	18.78
8–2	3.3	2.93	1.3	Fine sand	None	19.04
8–5	10.3	7.40	2.0	Very fine silt	None	22.92
8–6	6.7	−1.90	2.0	Granule	None	18.60
8–7	3.3	4.77	2.8	Coarse silt	None	19.42
8–10	.7	3.31	1.4	Very fine sand	None	17.94
9–2	3.3	5.12	3.2	Medium silt	None	18.33
9–5	4.2	7.55	2.0	Very fine silt	None	19.74
9–6	12.1	6.91	2.2	Fine silt	None	22.38
9–7	3.6	7.84	1.8	Very fine silt	None	20.05
9–8	4.2	4.35	2.6	Coarse silt	None	19.42
9–10	1.0	2.88	1.2	Fine sand	None	18.75
10–17	10.9	4.46	2.3	Coarse silt	None	23.77
10–18	.7	−.96	2.7	Very coarse sand	None	22.11
10–21	3.6	3.62	1.5	Very fine sand	None	22.81
Mean	3.8	[1] 5.37	2.1	Medium silt		19.60
Range	.7–12.1	−1.90–7.84	1.2–3.2			16.22–23.77

[1] Negative grain sizes excluded.

TABLE 5.—*Range of tolerance in ecological factors and geographical distribution of the five most commonly collected mollusks in Hillsborough Bay, Fla., August and September 1963*

Species	Temperature	Salinity	pH	Turbidity	Depth	Current	Sediment type	Bottom type	Distribution
	°C.	*P.p.t.*			*M.*	*Cm./sec.*			
Mulinia lateralis	[1 2] 1–34	[3] 1.4–75	[2] 6.8–8.7	Tolerant [2 3]	[4 5] 1–4.7	[5] 9.4–90	Nonselective; fine sand and silt.[5 6 7 8]	Unvegetated [3]	Maine to Florida and Gulf of Mexico.[9]
Amygdalum papyria	[1] 9–36	[10] 5–38	[2] 6.8–8.7	do [2 10]	[3 5] 1–4.7	[6] <90	Fine sand [5]	Unvegetated [5] Vegetated.	Maryland to Florida and Gulf of Mexico.[1 9]
Nassarius vibex	[1] 3–36	[1 11] 9–42	[2] 6.8–8.7	do [2 10]	[12] 1–15	[4 5] 8.6–90	Nonselective; sand and silt.[5 13]	Unvegetated [5 13] Vegetated.	Cape Cod to Florida and Gulf of Mexico.[9]
Tagelus plebeius	[1 2] 1–34	[1 7] 1–37	[2] 6.8–8.7	do [2]	[5 12] 1–4.7	[4 5] 30–90	Nonselective; sand and silt [5 14]	Unvegetated [5] Vegetated.	Cape Cod to Florida and Gulf of Mexico.[9]
Melongena corona	[2] 11–34	[15 16] 8–45	[2] 6.8–8.7	do [2 10]	[5 10] 1–4.7	[6] <90	Nonselective; shell, sand and silt [5 17]	Unvegetated [5 15 17]	Florida and Gulf of Mexico.[8 18]

[1] Parker, 1959.
[2] Saloman and Taylor, 1968.
[3] Breuer, 1962.
[4] Brett, 1963.
[5] This report.
[6] Taylor and Saloman, 1969.
[7] Hedgpeth, 1954.
[8] Marland, 1958.
[9] Abbott, 1954.
[10] Tabb, Dubrow, and Manning, 1962.
[11] Wells, 1961.
[12] Wass, 1965.
[13] Moore, Davies, Fraser, Gore, and Lopez, 1968.
[14] Allen, 1954.
[15] Tabb and Manning, 1961.
[16] Hathaway and Woodburn, 1961.
[17] Menzel, 1956.
[18] Hedgpeth, 1953.

Most of the healthy stations (60 percent) were at the mouth of Hillsborough Bay along transect 10. The most numerous and diverse mollusk assemblage was at station 10–15, where we collected 512 individuals and 17 species. At the upper end of the bay, conditions were healthy at stations C, C–2, and C–3 where more than average current (C–2 and C–3) and benthic algae (C, C–2, and C–3) maintain a favorable environment for many mollusks despite the proximity of effluent discharged from the Tampa Sewage Treatment plant at Hooker Point. Throughout the rest of the bay, all stations were either marginal or unhealthy (fig. 1).

The predominant sediment type at healthy stations was fine sand (2.80 Ø). Sediment sorting was poor (1.5 Ø), according to the classification of Folk (1964), and is a reflection of the weak current system in the bay (Taylor and Saloman, 1969). A number of authors have noted that fine sand is well suited for colonization by a variety of

mollusks (Jones, 1950; Pratt, 1953; Thorson, 1956; Sanders, 1958; McNulty, 1961; Brett, 1963). Another feature of most healthy stations was the occurrence of a red alga, *Gracilaria* sp., which is a source of organic detritus and provides a base for attachment of epiphytic mollusks.

Salinity at healthy stations was between 18 p.p.t. (upper bay stations C, C–2, and C–3) and 23 p.p.t. (transect 10). The combination of relatively high mollusk diversity and reduced salinity at the upper bay stations indicated that a factor other than salinity prevented the establishment of an equivalent variety of mollusks at most marginal and unhealthy stations.

MARGINAL STATIONS

At the 18 stations classified as marginal at least 50 percent of the live mollusks were indicator species, and the average incidence of indicators at these stations was 80 percent. The average number of species per station represented by live animals was only 3; the mean number of individuals was 102 (table 3). In comparison with the healthy stations, marginal stations had about one-fourth as many species of mollusks and about one-half as many individuals.

Sediments at marginal stations ranged from fine sand to medium silt. The average sediment type was very fine sand (3.09ϕ)—a somewhat finer particle size than the average size at healthy stations. Sediment sorting was poor (1.4ϕ) and very close to the figure for healthy stations.

Bottom vegetation (*Gracilaria* sp.) was found at only one marginal station. That station had a substrate of fine sand and more species of mollusks than any other station.

Low salinity (less than 4 p.p.t.) near the mouth of the Alafia River was probably responsible for fewer species of mollusks at stations C–8, C–8–1, and C–8–2. The only species present in this area was *Tagelus plebeius*.

Data for DO (dissolved oxygen) indicated that from June through August bottom water in the bay between transect 10 and McKay Bay becomes anaerobic (FWPCA, personal communication; see footnote 3). At other times, however, DO values are generally above 3 ml./liter and would not prove limiting. Changes in the DO at stations regarded as marginal may create a more favorable environment for mollusks during other seasons.

UNHEALTHY STATIONS

No live mollusks were collected at 19 stations classified as unhealthy (fig. 1). Two of these stations were on the eastern shore of the bay (8–10 and 9–10) and adjacent to an extensive area of gypsum spoil—a byproduct of the phosphate industry. The gypsum forms a crust on the bottom that virtually eliminates macrobenthic organisms.

Sediments at other unhealthy stations had a mean grain size that varied from −1.90 ϕ (granule) to 7.84 ϕ (very fine silt)—see table 4. Sediments were coarse at stations near spoil islands left from channel construction and on a natural, shelly shoal (C–7). Absence of mollusks in coarse sediments probably resulted from the grinding action of large particles powered by wave action. Stations with fine sediments were in comparatively deep water. There the sediments had a high concentration of the toxic compound, hydrogen sulfide, and are probably anaerobic, or nearly so, at all times (Florida State Board of Health, 1965).

ECOLOGICAL ZONES

Isopleths were drawn between similar stations to represent approximate boundaries of healthy, marginal, and unhealthy zones in Hillsborough Bay (fig. 2). Calculation of the area within each zone showed that only 22 percent of the bay falls in the healthy category, 36 percent is marginal, and 42 percent is unhealthy. Most healthy zones were near the mouth of the bay where the solid and soluble products of pollution were least concentrated. Marginal zones were on the bottom slopes between the three unhealthy zones that were along the eastern and western shores and in midbay ship channels. Observations in Raritan Bay (Dean and Haskin, 1964) and Biscayne Bay (McNulty, 1966) suggest that pollution abatement in Hillsborough Bay would favor progressive repopulation of marginal zones by a more normal assemblage of benthic plants and animals. In heavily silted areas of the unhealthy zones, however, biological restoration would probably require a long period of time.

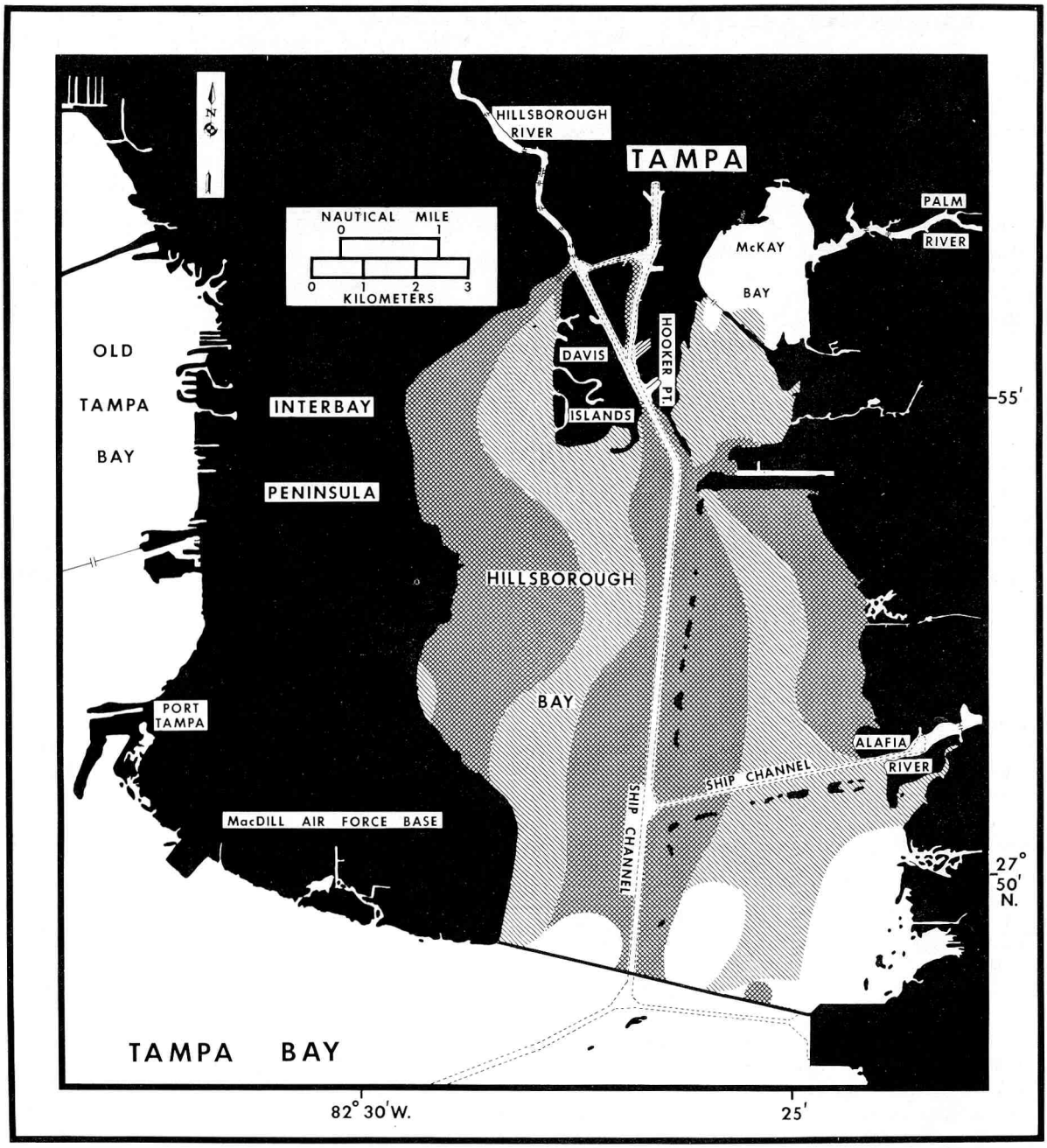

FIGURE 2.—Ecological zones in Hillsborough Bay, Fla., based on the comparative diversity of mollusks—healthy zone (unshaded); marginal zone (hatching); unhealthy zone (cross hatching)—August and September 1963.

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APPENDIX

A CHECKLIST OF MOLLUSKS FOUND IN HILLSBOROUGH BAY, FLORIDA, AUGUST AND SEPTEMBER 1963

We collected and identified 64 species of mollusks representing 43 families. Determinations were based on standard taxonomic works (Abbott, 1954; Perry and Schwengel, 1955; Warmke and Abbott, 1962; Keen, 1963; Abbott, 1968) and by comparison with specimens in the U.S. National Museum (+). An asterisk (*) indicates that the species was collected alive.

Class Gastropoda

Family Neritidae
Neritina reclivata (Say)
Family Rissoidae
Rissoina chesneli Michaud
Family Vitrinellidae
Cyclostremiscus sp.
Family Cerithiidae
**Bittium varium* (Pfeiffer)
Seila adamsi (H. C. Lea)
Family Triphoridae
Triphora nigrocincta (C. B. Adams)

Family Epitoniidae
**Epitonium angulatum* (Say)
**Epitonium humphreysi* (Kiener)
Epitonium rupicola (Kurtz)
Family Calyptraeidae
**Crepidula fornicata* (Linné)
**Crepidula plana* Say
Family Naticidae
**Natica pusilla* Say
**Polinices duplicatus* (Say)
Family Muricidae
**Urosalpinx tampaensis* (Conrad)
Family Columbellidae
**Anachis obesa* (C. B. Adams)
+Anachis semiplicata (Stearns)
**Mitrella lunata* (Say)
Family Melongenidae
**Melongena corona* (Gmelin)
Family Nassariidae
**Nassarius vibex* (Say)
Family Olividae
Olivella perplexa Olsson
Family Marginellidae
Prunum apicinum (Menke)
Family Atyidae
**Haminoea succinea* (Conrad)
Family Retusidae
**Retusa canaliculata* (Say)
Family Pyramidellidae
*+*Odostomia acutidens* Dall
Odostomia impressa (Say)
+Odostomia producta (Dall)
+Turbonilla conradi Bush.
Family Acteocinidae
Cylichna bidentata (Orbigny)
Family Acteonidae
**Acteon punctostriatus* (C. B. Adams)
Family Ellobiidae
Melampus coffeus (Linné)

Class Amphineura

Family Ischnochitoniidae
**Ischnochiton papillosus* (C. B. Adams)

Class Pelecypoda

Family Nuculidae
**Nucula proxima* Say
Family Nuculanidae
Nuculana acuta Conrad
Family Arcidae
**Anadara transversa* (Say)
Family Mytilidae
**Amygdalum papyria* (Conrad)
**Brachidontes exustus* (Linné)
**Modiolus americanus* (Leach)
Modiolus demissus granosissima (Sowerby)
Family Pinnidae
Atrina rigida (Lightfoot)
Family Ostreidae
**Crassostrea virginica* (Gmelin)
Family Carditidae
Cardita floridana Conrad
Family Corbiculiidae
**Polymesoda caroliniana* (Bosc)
Family Leptonidae
**Mysella planulata* (Stimpson)
Family Cardiidae
**Laevicardium mortoni* (Conrad)
Family Veneridae
Chione cancellata (Linné)
**Mercenaria campechiensis* (Gmelin)
Parastarte triquetra (Conrad)
Family Petricolidae
Petricola pholadiformis Lamarck
Family Tellinidae
Macoma constricta (Bruguière)
**Macoma tenta* Say
Tellina alternata Say
Tellina lineata Turton
**Tellina versicolor* DeKay
Family Semelidae
Semele bellastriata (Conrad)
Semele proficua (Pulteney)
Family Donacidae
Donax variabilis Say
Family Sanguinolariidae
**Tagelus divisus* Spengler
**Tagelus plebeius* (Lightfoot)
Family Solenidae
**Ensis minor* Dall
Family Mactridae
Mactra fragilis Gmelin
**Mulinia lateralis* (Say)
Family Corbulidae
**Corbula barratiana* C. B. Adams
**Corbula caribaea* Orbigny
Family Pholadidae
Cyrtopleura costata (Linné)
Family Lyonsiidae
Lyonsia hyalina floridana Conrad
Family Thraciidae
**Thracia* sp.

MIGRATION OF JUVENILE SALMON AND TROUT INTO BROWNLEE RESERVOIR, 1962–65

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ABSTRACT

Migrations of juvenile chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), sockeye and kokanee salmon (*O. nerka*), and rainbow trout (*Salmo gairdneri*) from the Snake and Weiser Rivers and from Eagle Creek were studied. Populations of fish were sampled with floating traps above the reservoir and a fixed louver trap in Eagle Creek near the lower end of Brownlee Reservoir. Age and length of fish, timing of migration, and numbers of fish of native or hatchery origin were determined. This information was needed to evaluate the effect of Brownlee Reservoir on migrations of anadromous fish.

Brownlee Reservoir was created when a high-head hydroelectric dam was built in 1958 at the upstream end of Hells Canyon on the Snake River. The 92-km. long reservoir forms part of the boundary between Idaho and Oregon. At full pool, it is 92 m. deep and less than 1 km. wide; the upper end (22 km.) is relatively shallow and essentially riverine.

BCF (Bureau of Commercial Fisheries) chose Brownlee Reservoir for an extensive research program to determine how a large impoundment affects the passage of salmon and trout. The research, begun in the spring of 1962, comprised five studies: (1) limnology of the reservoir system (Ebel and Koski, 1968), (2) upstream migration of adult chinook salmon (*Oncorhynchus tshawytscha*) through the reservoir (Trefethen and Sutherland, 1968), (3) migration of juvenile salmon and trout into the reservoir (this report), (4) distribution and movement of juvenile salmon in the reservoir (Durkin, Park, and Raleigh, 1970), and (5) migration of juvenile salmon and trout from the reservoir (Sims, 1970).

Three major streams—the Snake, Burnt, and Powder Rivers—and more than a dozen minor streams, most of which have intermittent flows, are tributaries to Brownlee Reservoir. Previous investigations had shown that most of the streams supported local populations of rainbow trout (*Salmo gairdneri*), but chinook salmon and steelhead trout (the anadromous form of rainbow trout) spawned in only three of the streams. Spring- and fall-migrating steelhead trout and spring-migrating chinook salmon spawned in Eagle Creek, a tributary of the Powder River, and in the Weiser River, a tributary of the Snake River (fig. 1). Fall-migrating chinook salmon spawned in the Snake River about 257 km. above the dam.

Wild (native) salmon and trout fingerlings entered the reservoir during each year of study (1962–65). From 1963 on, most of the chinook salmon spawners were diverted to a hatchery. In 1964 and 1965, therefore, hatchery-reared progeny of fall chinook salmon from the lower Columbia River were released in the Snake River spawning area above the reservoir. We wished to study the effect of a large impoundment on other species of salmon, so yearling coho (*O. kisutch*) from the lower Columbia River and sockeye salmon (*O. nerka*) from the Skeena River were included in the hatchery releases in 1964 and 1965, respectively. In 1963, 1964, and 1965, migrations of wild kokanee (*O. nerka*) entered the reservoir from the Payette River system.

This report provides estimates of age and length of fish from each population at the time of entry into the reservoir, time and duration of downstream migrations, and numbers of fish of native and hatchery origin for 1962 through 1965.

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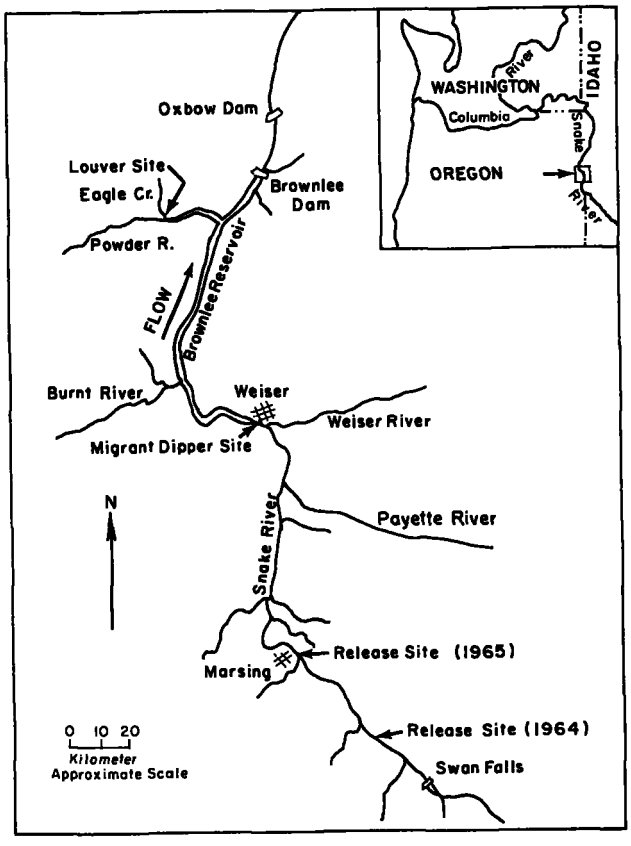

FIGURE 1.—Study area showing locations of sampling equipment used to assess migrations of juvenile salmon and rainbow trout to Brownlee Reservoir.

SAMPLING SITES, EQUIPMENT, AND PROCEDURES

The plan of study was to sample populations of migrating fish before they entered the reservoir, to determine their characteristics, and to estimate their abundance. This plan required the installation of floating fingerling traps in the Snake River above the reservoir and a fixed louver in Eagle Creek, a tributary of the Powder River near the lower end of Brownlee Reservoir (fig. 1).

Sample catches from the populations of juvenile chinook salmon in the Snake and Weiser Rivers early in the study established that juvenile fall chinook salmon migrated from the Snake River at age 0, whereas juvenile spring chinook salmon migrated from the Weiser River at age 1. Thus, it was possible to separate these two populations on the basis of age or size and to sample them from a single location below the confluence of the two rivers.

SNAKE RIVER

The sampling site for the Snake and Weiser Rivers was about 8 km. below their confluence and about 4 km. above the reservoir. Flows during the spring were 383 to 1,372 c.m.s. (cubic meters per second) and averaged 744 c.m.s. At average flow, the Snake River channel at this location was about 152 m. wide and had a maximum depth of 7.6 m.

The sampling device in the Snake River was a modified "migrant dipper" (Mason, 1966)—a self-cleaning, floating fingerling trap with louvered leads (fig. 2). The basic unit consisted of a trap section, 12.2 m. long by 7.6 m. wide by 1.8 m. deep, with fixed louver leads that extended 9.8 m. upstream at a 10° angle to the flow. A self-cleaning traveling screen formed the rear of the trap, and a metal screen floor extended upstream to the two fixed louver sections. The louvers guided the fish into the trap area where a continuously rotating scoop dipped the fish and deposited them into a trough. The fish were then flushed into a holding pen at the side of the trap.

Fish were captured in traps from 1962 through 1965. We carried out feasibility tests with one trap in 1962 and examined the horizontal distribution of downstream migrants at the same time. In the spring of 1963, two migrant dipper traps were attached to an overhead cable and positioned in the main current. Floating louver extensions were added to the fixed louver sections to increase the sampling capability. In attempts to increase the catch, the louver angle and lengths were altered each year (table 1). In 1962, the traps were operated continuously from mid-April until early July and then intermittently until December. On the basis of these early experiments, the operations in 1963–65 began in mid-March and ended in July.

TABLE 1.—*Traps used in the Snake River and configuration of attached louver arrays*

Year	Traps	Details of louver leads		
		Angle	Length	Width at mouth
	Number	*Degrees*	*M.*	*M.*
1962	1	10	9.7	13.7
1963	2	30	22.0	30.5
1964	2	15	22.0	21.4
1965	1	15	47.6	30.5

Fish captured in the traps and subsequent estimates of the magnitude of migration were classi-

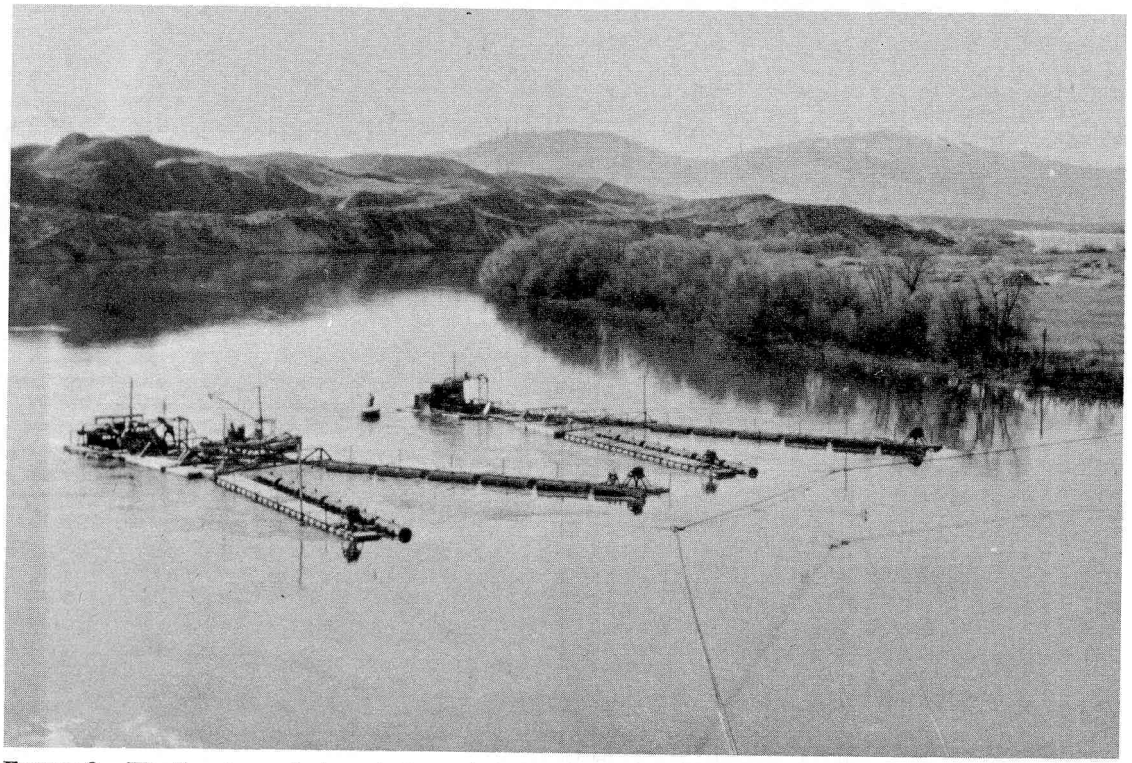

FIGURE 2.—Floating traps (migrant dippers) used to sample migrations of juvenile salmon and rainbow trout in the Snake River above Brownlee Reservoir.

fied by age group on the basis of lengths determined by daily sampling. The length-age relation was established by scale analysis. Fingerlings in their first year of life are termed age-group 0; these fish become age-group I on January 1 of the succeeding year.

Marked fish were used to estimate the proportion of the migration captured by the traps. The proportion varied with trap design and position, size and species of migrants, and flow and turbidity of the river. A portion of the daily catch of fish was marked, transported 3.2 km. upstream, and released for recapture. They were marked by age group and released at scheduled intervals during the day and night.

Fish marked to assess the migration from the Snake River were tattooed (Volz and Wheeler, 1966). This method provided many combinations of marks that were durable and could be easily detected. Juvenile salmon from each population were fin-clipped or jaw-tagged each year for subsequent identification as they moved through the reservoir.

EAGLE CREEK

The sampling site at Eagle Creek was 183 m. upstream from its confluence with the Powder River and about 460 m. from the reservoir (fig. 1). The stream at this point was 15 m. wide at normal flows. Except during maximum runoff in the spring, flows seldom exceeded 57 c.m.s.

Samples of downstream migrants were obtained with a stationary louver device (Bates and Vinsonhaler, 1957)—see figure 3. In 1962, the louver (18.3 m. long and 0.9 m. high) was positioned at a 30° angle to the stream bank. In 1963, to increase the catch and eliminate selectivity for larger fish, the angle was decreased to 15° and the length extended to 36.6 m. In 1964, the channel was altered above the louver to straighten the approach flow.

Fish from Eagle Creek were collected from three sources and marked in a variety of ways. Most fish were stained with Bismark Brown Y dye [1] (Deacon, 1961) and released above the sam-

[1] Trade names referred to in this publication do not imply endorsement of commercial products by the Bureau of Commercial Fisheries.

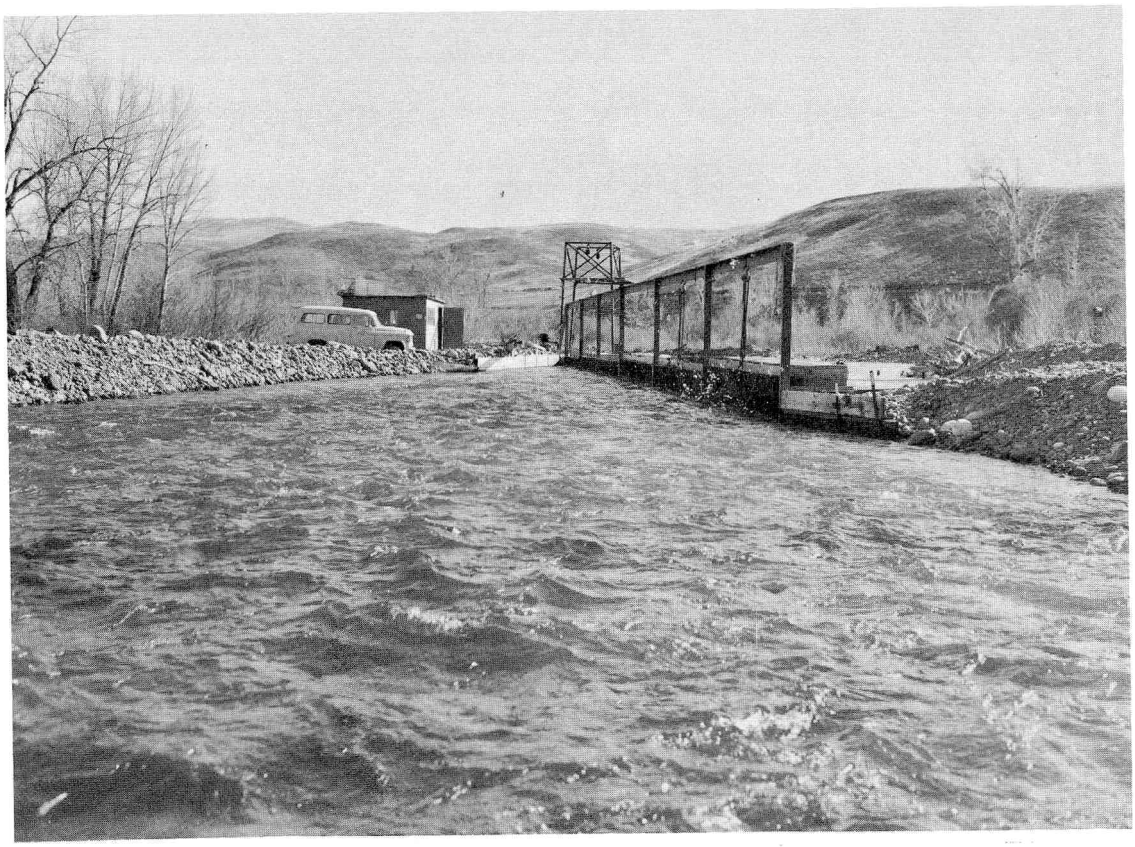

FIGURE 3.—Stationary louver used to estimate the number of juvenile salmon and rainbow trout migrating into Brownlee Reservoir from Eagle Creek.

pling site to determine trapping efficiencies of the louver. Fish to be stained could be held in the cooler waters of Eagle Creek with little difficulty, whereas they could not be kept alive for sufficient time to stain them in the warmer waters of the Snake River. We obtained test fish mainly from irrigation bypass traps and fyke nets located several kilometers upstream. When sufficient numbers of migrating fish were not available from these sources, we used fingerlings captured at the louver. Periodically, groups of migrants from Eagle Creek were marked by fin-clipping, jaw tags, or plastic thread tags [2] for identification in the reservoir.

DOWNSTREAM MOVEMENT, AGE, LENGTH, AND TIME OF ENTRY INTO THE RESERVOIR OF JUVENILE SALMON AND TROUT

The characteristics of the migrations into Brownlee Reservoir were determined from catches at the sampling sites. Timing and peaks of runs are expressed as weekly percentages of the estimated numbers of fish in the migrations. About 10 percent of each daily catch was examined for data on length and age.

[2] Developed by the Fish Commission of Oregon.

MIGRATIONS OF WILD SALMON AND TROUT

Migrations of wild chinook salmon and steelhead trout juveniles entered the reservoir from three tributaries. Fall chinook entered from the Snake River, whereas spring chinook and steelhead entered from Eagle Creek and Weiser River.

Fall Chinook Salmon

The movement of juvenile fall chinook salmon from the Snake River to Brownlee Reservoir began about mid-April and peaked in mid-May in 1962 and 1963 (fig. 4). About 75 percent of the migration took place during a 2-week period, and nearly all of the fish had migrated by mid-June. Principal movement was between sunrise and 10 a.m. and from 3 to 7 p.m.

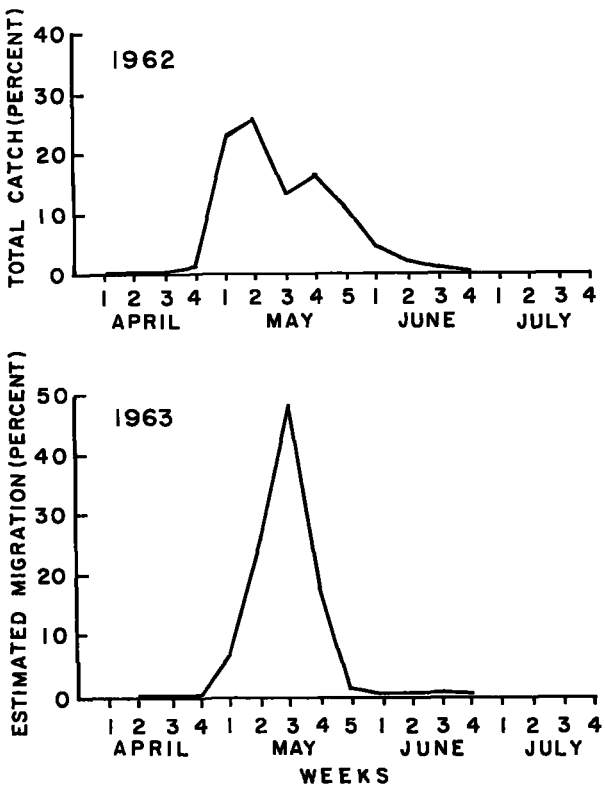

FIGURE 4.—Timing of migration of native juvenile fall chinook salmon (age-group 0) from the Snake River to Brownlee Reservoir by weekly periods, 1962–63.

The size of native juvenile fall chinook salmon increased throughout the migration period (table 2). Early migrants in 1962 averaged 52 mm.; by the final week, average length had increased to 71 mm. The migrants averaged larger in 1963—73 mm. at the start and 81 mm. at the end of the migration period.

Spring Chinook Salmon

Spring chinook salmon enter Brownlee Reservoir from Weiser River and Eagle Creek; their season of spawning is similar, but the sizes and seasons of migration of the juveniles into the reservoir are substantially different.

Weiser River population.—Juvenile spring chinook salmon from the Weiser River first appeared at the Snake River trap in early April and peaked in late April or early May (fig. 5). The migration was nearly complete by late May in all years. Daily catches of spring chinook salmon were greatest between 7 and 11 a.m. and 3 and 7 p.m. except during the peak when diurnal highs were not

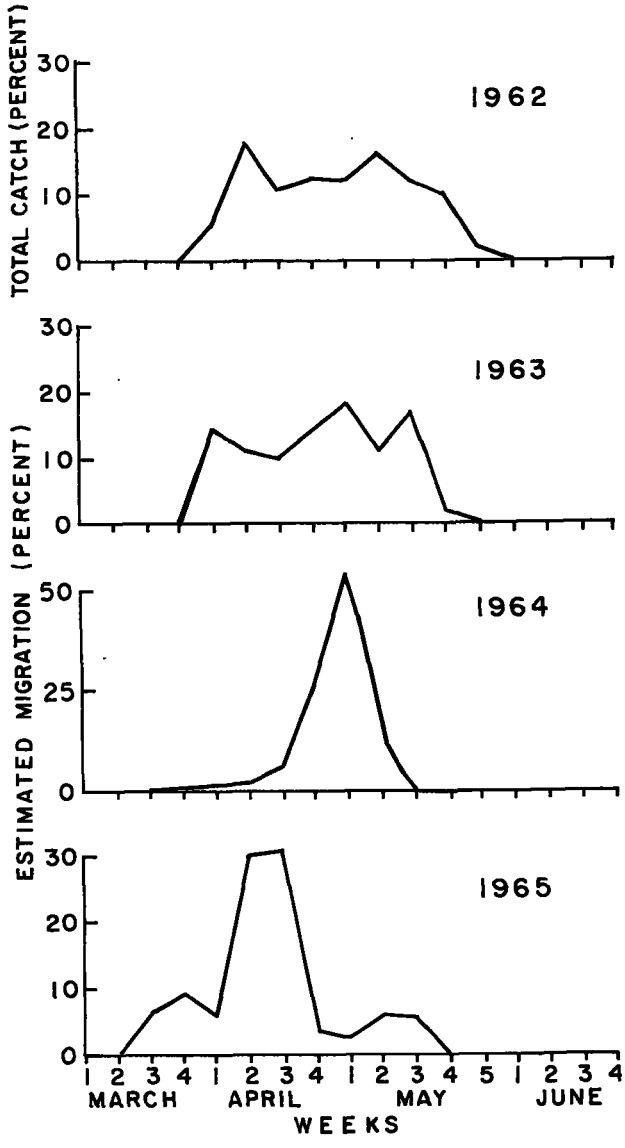

FIGURE 5.—Timing of migration of juvenile spring chinook salmon from the Weiser River to Brownlee Reservoir by weekly periods, 1962–65.

clearly defined. Daily catches were lowest between 10 p.m. and 4 a.m.

The size of spring chinook salmon from the Weiser River differed from that of wild fall chinook salmon from the Snake River in 1962–63; spring fish were age-group I and distinctly larger than fall fish, which were age-group O. In 1964 and 1965, however, the difference between these wild spring chinook salmon and the hatchery-reared fall chinook salmon was less apparent by late April when the length ranges merged. In

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TABLE 2.—*Lengths of wild juvenile fall chinook salmon from the Snake River during migration past sampling site, 1962–64*

Year	Length of fish at stage of migration					
	Early [1]			Late [2]		
	Fish	Mean	Range	Fish	Mean	Range
	Number	*Mm.*	*Mm.*	*Number*	*Mm.*	*Mm.*
1962	76	52	33–80	434	71	47–103
1963	97	73	48–99	133	81	67–98
1964	[3]			146	79	61–90

[1] Mid-April to mid-May.
[2] Mid-May to mid-June.
[3] No discernible fish of this group in sample.

1964 and 1965, the two populations were separated by the percentage of each age group in the daily sample as estimated from scale analysis.

The average length of spring chinook salmon varied from 106 mm. in 1962 to 149 mm. in 1964 (table 3). Each year the average size increased from the beginning to the end of the migration.

A few large individuals (215–260 mm.) were captured in 1963 and 1964, but the total constituted less than 1 percent of the catch. These fish (age-group III) appeared at the trap early in the season during extremely high flows from the Weiser River.

TABLE 3.—*Lengths of juvenile spring chinook salmon from the Weiser River during migration past sampling site in the Snake River, 1962–65*

Year	Length of fish at stage of migration					
	Early [1]			Late [2]		
	Fish	Mean	Range	Fish	Mean	Range
	Number	*Mm.*	*Mm.*	*Number*	*Mm.*	*Mm.*
1962	8	106	95–117	104	134	125–151
1963	438	108	94–140	52	142	116–155
1964	249	112	100–145	81	149	126–165
1965	19	119	101–130	22	140	120–155

[1] April to peak of migration (late April or early May).
[2] From peak of migration through May.

Eagle Creek population.—Juvenile spring chinook salmon from Eagle Creek migrated downstream most of the year except during the summer when flows averaged less than 1 c.m.s. (fig. 6). The principal migration was in the fall when flows at the trapping site exceeded 1.5 c.m.s. As irrigation was reduced at this time, most of the flow remained in the stream channel, and water temperatures ranged from 0° to 13° C. Winter migrations were small and occurred only during short-term increases in water temperature and flow. A secondary migration took place in the spring as water temperature and flows again increased. The migration declined just before high flows from spring rain and melting snow (fig. 6). Periodic sampling during the high flows suggested that few chinook salmon were migrating. As water levels receded, however, fish were taken in limited numbers until the upstream diversion of water for irrigation greatly reduced the flows at the louver. Water temperatures increased in the spring from near freezing to about 8° C.

Chinook salmon of age-group 0 dominated the migration in the fall. These fish emerged from the gravel in the spring and were the offspring of adults that had spawned in late summer and early fall of the previous year. The size of the 0-group fish varied slightly from year to year and throughout the migration period (table 4).

Juvenile chinook salmon that moved downstream from January into late spring were primarily age-group I fish. A small number of age-group 0 (average, 60 mm.; range, 41–80 mm.) was sampled from April through June 1963. Some age-group II fish—less than 3 percent of the total

TABLE 4.—*Lengths of juvenile spring chinook salmon at beginning and end of spring and fall migrations at Eagle Creek, 1962–65*

Year	Spring migration								Fall migration							
	Age-group 0				Age-group I				Age-group 0				Age-group I			
	Beginning		End		Beginning		End		Beginning		End		Beginning		End	
	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1962	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	78	53–109	84	60–111	119	112–120	132	[2] 115–168
1963	[3]	[3]	61	45–80	86	65–105	93	71–98	87	64–118	89	60–116	144	130–152	[3]	[3]
1964	[3]	[3]	66	58–78	90	72–108	94	72–130	102	76–121	103	78–125	158	—158	[3]	[3]
1965	[3]	[3]	[2]	[2]	100	86–118	111	83–119	108	83–119	[1]	[1]	[1]	[1]	[1]	[1]

[1] Not in operation.
[2] Few fish sampled.
[3] Not in catches.

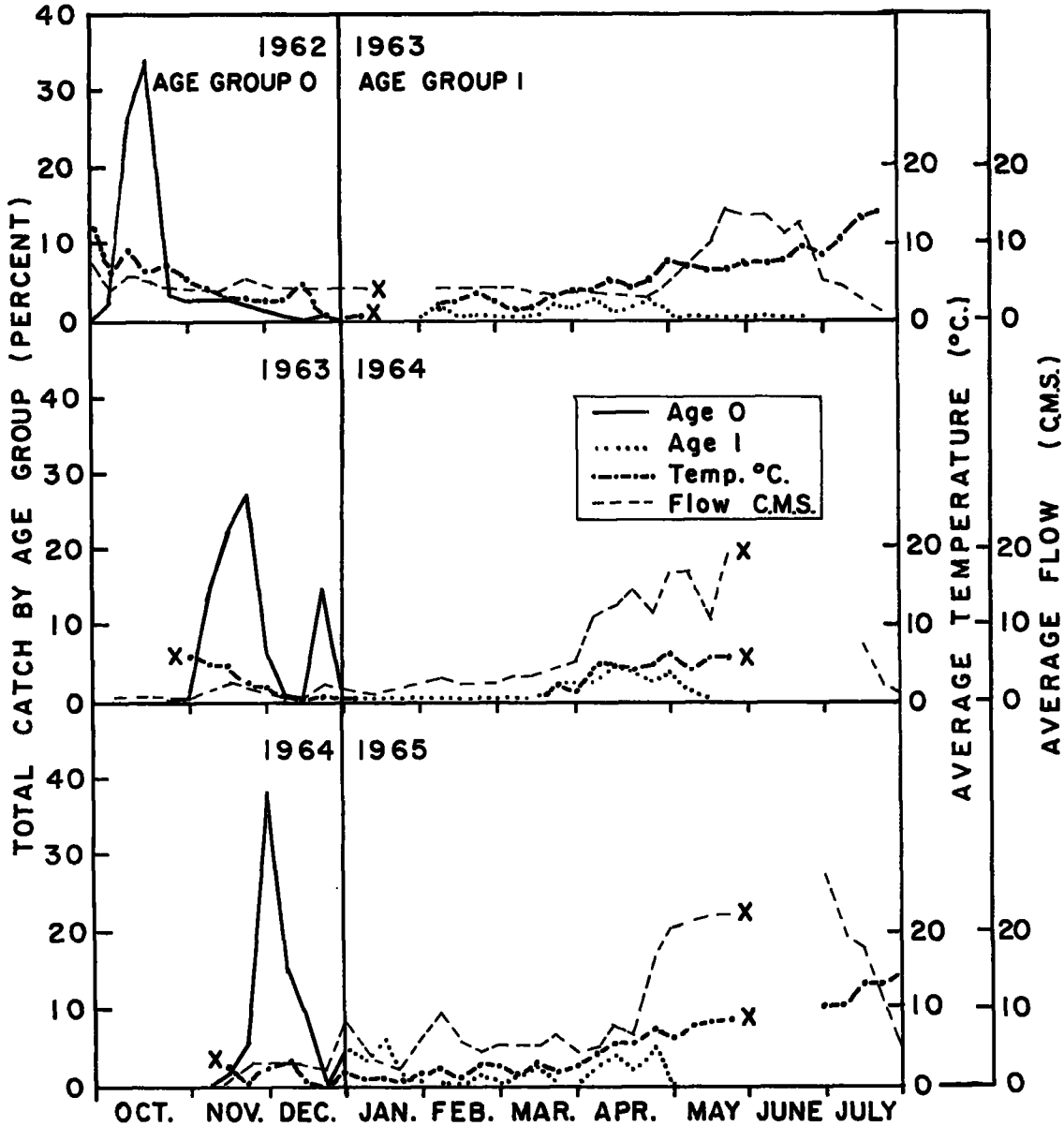

FIGURE 6.—Timing of migration of spring chinook salmon (age-groups O and I) from Eagle Creek to Brownlee Reservoir in relation to water temperature and flow, 1962–65 (x indicates periods of no data).

catch—were taken each spring. These fish averaged 140 mm. (126–180 mm.) and were scattered throughout the migration.

Most fish moved downstream past the louver at night—between 6 and 12 p.m. Few fish were caught through the rest of the 24-hour period except during high flows and turbid water; at these times fish moved downstream throughout the day and night.

Kokanee

Kokanee salmon from the Payette River system appeared at the Snake River sampling site in mid-June in 1963–65. The migration was evident for 3 or 4 weeks, but most of the fish moved downstream during a 1-week period (fig. 7). Kokanee averaged 118 to 120 mm. long through the 1964 migration and 93 to 108 mm. through the 1965 season (table 5).

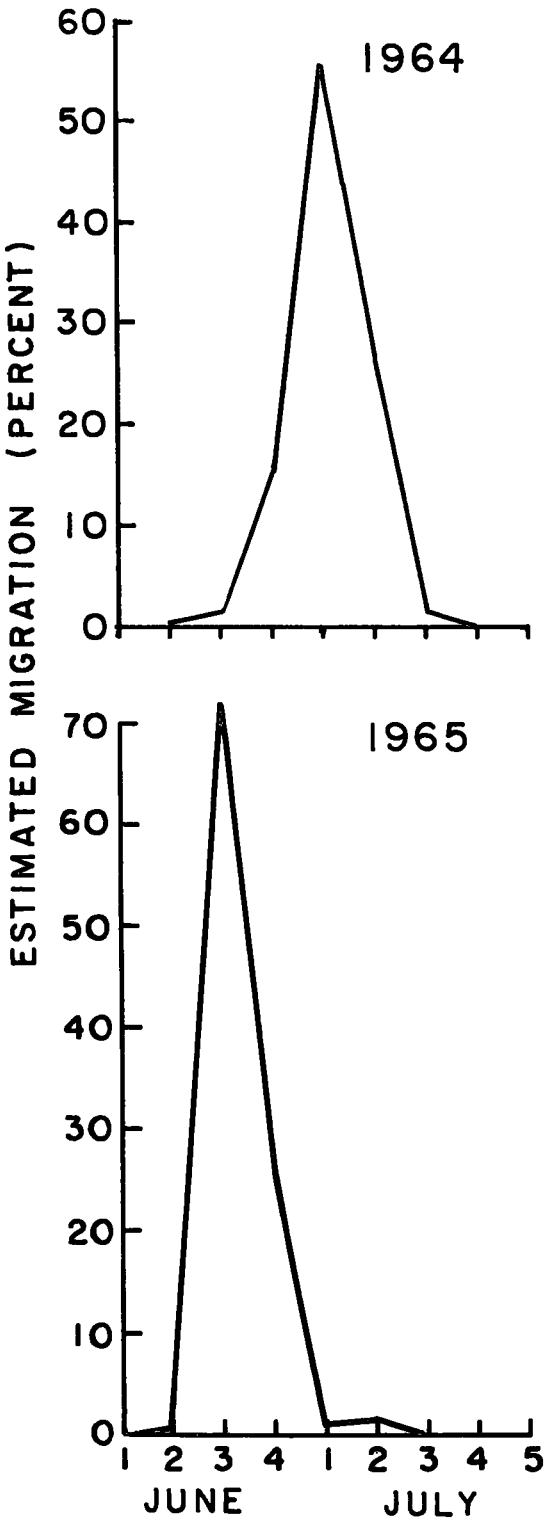

FIGURE 7.—Timing of migration of kokanee salmon from the Snake River to Brownlee Reservoir, 1964–65.

Rainbow Trout

Anadromous rainbow trout spawned in the same tributaries as spring chinook salmon. Offspring of the anadromous form could not be separated from resident native and planted rainbow trout that complete their life cycle in fresh water. Studies on the entry of trout into the reservoir included young from all three groups.

TABLE 5.—*Lengths of juvenile kokanee salmon during migration past sampling site in Snake River, 1963–65*

Year	Length of fish at stage of migration					
	Early [1]			Late [2]		
	Fish	Mean	Range	Fish	Mean	Range
	Number	*Mm.*	*Mm.*	*Number*	*Mm.*	*Mm.*
1963	7	[3]	100–110	3	[3]	128–142
1964	279	118	88–140	107	120	104–146
1965	166	93	80–110	151	108	70–155

[1] First week.
[2] Last week.
[3] Insufficient sample.

Trout migrated from the Snake River in the spring (fig. 8) at the same time as the chinook salmon populations. Time of peak migration varied but was in late April or May 1962–65. Age groups were from O to IV, but most were age-group I and II. Size overlap was considerable among age-groups I and II. Table 6 shows the age groups and length-frequency ranges for 1963.

The movement of rainbow trout from Eagle Creek (fig. 9) also took place primarily in the spring; about 75 percent of the fish migrated in late spring, at a time of high flows. A smaller run peaked in the fall. Fish of age-groups I and II dominated the run in the spring. Age-groups O and I were dominant in the fall; however, all age-groups O through IV were represented. Table 7 shows the size ranges.

MIGRATIONS OF HATCHERY-REARED SALMON

Most of the chinook salmon spawners were diverted to hatcheries from 1963 through 1965. In 1964 and 1965, hatchery-reared fingerling salmon were released at the Snake River spawning area, 88 to 120 km. above the reservoir. Chinook salmon fingerlings from fall migrating adults were released in 1964 and 1965. Coho salmon fingerlings were released in 1964 and sockeye salmon fingerlings in 1965.

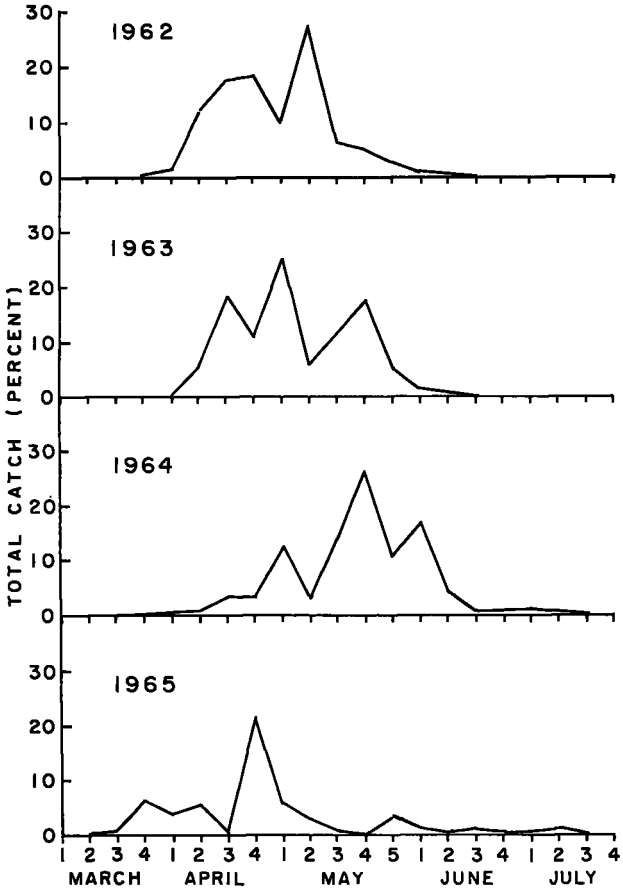

FIGURE 8.—Timing of migration of juvenile rainbow trout to Brownlee Reservoir from the Snake River, 1962–65.

TABLE 6.—*Age groups and lengths of juvenile rainbow trout captured in the migrant dipper traps in the Snake River above Brownlee Reservoir in 1963*

Age group	Fish	Mean length	Range
	Number	*Mm.*	*Mm.*
0	2	(1)	95–100
I	502	177.1	125–210
II	276	239.8	190–285
III	34	294.1	275–340
IV	1	(1)	382

[1] Insufficient sample.

TABLE 7.—*Age groups and lengths of juvenile rainbow trout from Eagle Creek during migration past sampling site in fall 1962*

Age group	Fish	Mean length	Range
	Number	*Mm.*	*Mm.*
0	119	78.0	52–109
I	228	141.7	90–183
II	16	200.0	180–265
III	3	(1)	225–270
IV	1	(1)	285

[1] Insufficient sample.

Fall Chinook Salmon

Hatchery-reared juveniles of fall chinook salmon were released in the Snake River above the reservoir in 1964 and 1965 to supplement the dwindling smolt migrations of wild fall chinook salmon. About 250,000 fall chinook salmon were released 120 km. above the reservoir from March 30 to April 3, 1964, when water temperatures averaged 9.5° C. In 1965, 592,000 juvenile fish were released 88 km. upstream from the reservoir from March 15 to 25, when the water temperature averaged 9.8° C. A tank truck transported the fish from hatcheries on the lower Columbia River. The fish were released during daylight.

The migrations of hatchery chinook salmon overlapped with migrations of wild spring chinook (age-group I) from the Weiser River. In 1964, juvenile chinook salmon from hatchery releases were recovered at the Snake River sampling site within 3 days after the first release. Downstream migration continued until late June, but catches were highest in mid-May (fig. 10). The migration in 1965 was longer and the peak less well defined.

The lengths of hatchery-reared chinook salmon increased as the season progressed and by late April were the same size as those of the age-group I wild chinook salmon from Weiser River. The hatchery fish captured at the migrant dipper in 1964 averaged 74 mm. (56–100 mm.) early in the season and 112 mm. (91–135 mm.) near the end of the migration (table 8). In 1965, the hatchery fish averaged 69 mm. (46–90 mm.) at the start of migration and 112 mm. (96–125 mm.) at the end.

TABLE 8.—*Lengths of hatchery-reared juvenile chinook salmon during migration past sampling site in Snake River, 1964–65*

Year	Length of fish at stage of migration					
	Early [1]			Late [2]		
	Fish	Mean	Range	Fish	Mean	Range
	Number	*Mm.*	*Mm.*	*Number*	*Mm.*	*Mm.*
1964	264	74.5	56–100	220	112	91–135
1965	125	69.3	46–90	124	112	96–125

[1] March through mid-May.
[2] Mid-May through June.

Coho Salmon

The introduction of 375,000 juvenile coho salmon into the Snake River in 1964 provided an

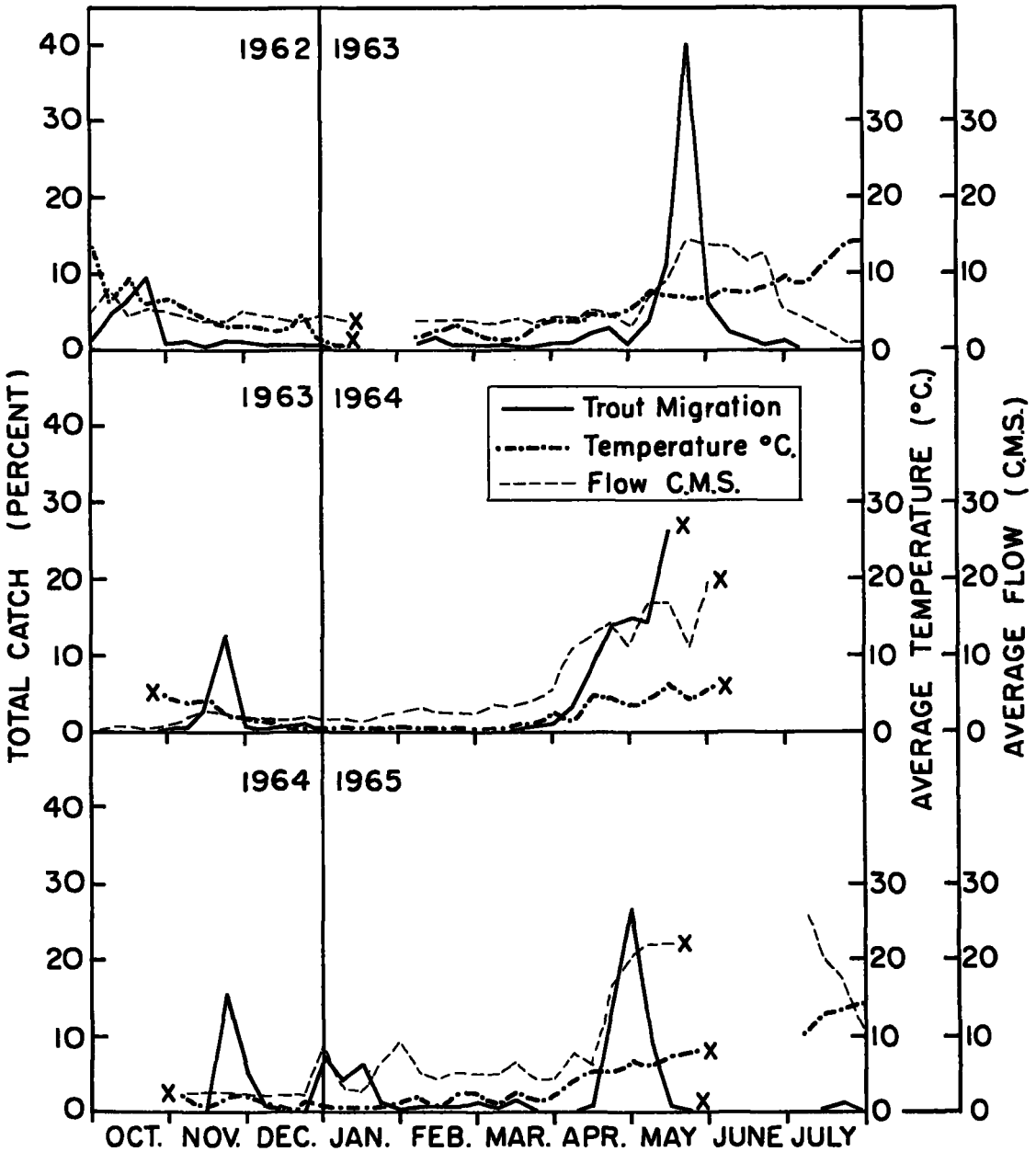

FIGURE 9.—Timing of migration of juvenile rainbow trout to Brownlee Reservoir from Eagle Creek in relation to water temperature and flow, 1962–65 (x indicates period of no data).

opportunity to study the migration of a nonindigenous species. These fish were obtained from a hatchery in the lower Columbia River, transported 120 km. above the reservoir, and released from March 15 to 30 in water that averaged 9.4° C. They did not appear in the Snake River trap until mid-April (fig. 11). The run peaked in mid-May and ended in early June.

The mean lengths of trap samples of coho salmon increased throughout the migration. Migrants averaged 112 mm. (71–140 mm.) early in the season; by the end of the migration period they averaged 131 mm. (110–166 mm.).

Sockeye Salmon

About 473,000 sockeye salmon fingerlings were released in 1965 in the Snake River 88 km. above

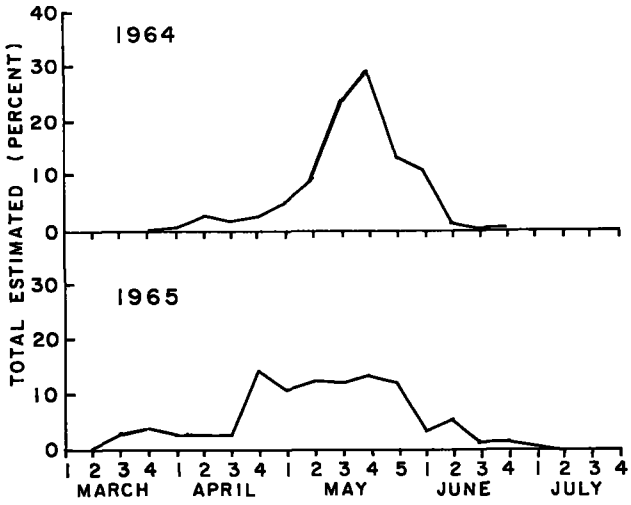

FIGURE 10.—Timing of migration of juvenile hatchery-reared fall chinook salmon (age-group 0) to Brownlee Reservoir from the Snake River, 1964–65.

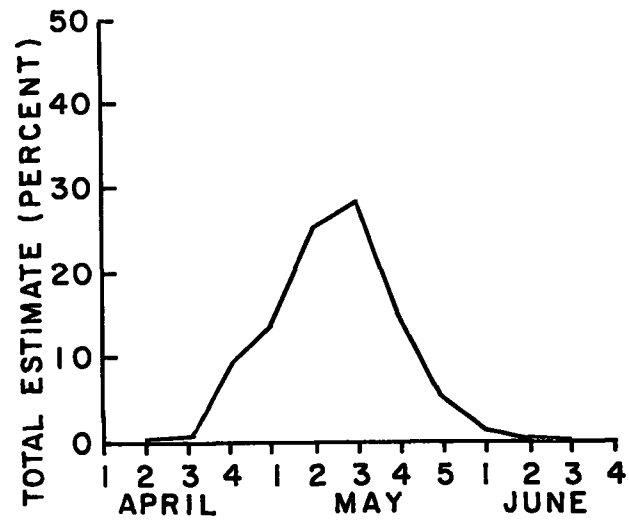

FIGURE 11.—Timing of migration of juvenile hatchery-reared coho salmon from the Snake River to Brownlee Reservoir, 1964.

the reservoir. These fish were reared from eggs obtained in the fall of 1963 from Babine Lake, British Columbia. The eggs were eyed at a hatchery at Maurice Lake, British Columbia, and transported to Leavenworth National Fish Hatchery in Washington, where they were reared until their release in 1965. Releases of 20,000 to 30,000 fish were made 5 days each week from March 15 to April 8, 1965; river water temperatures averaged 9.8° C. The sockeye salmon moved rapidly downstream; the first migrants were recovered within 2 days after the initial release. Peak migration was during the first week of April (fig. 12); by mid-April the migration was nearly complete. Sockeye salmon migrants averaged 121 mm. long (86–175 mm.).

UPSTREAM MOVEMENTS OF JUVENILE CHINOOK SALMON

A late group of chinook salmon fingerlings appeared at the Snake River trap near the end of June or in early July of each year. Because the migrations of fall- and spring-run chinook salmon were essentially completed by this time, the origin of these fish was of interest. Their length was similar to that of age-group I fish from the Weiser River, but examination of their scales revealed that they were fingerlings of age-groups O and I. Growth patterns on their scales showed an area of rapid growth at the margin typical of fish from the reservoir. This scale structure indicated they had moved upstream from the reservoir. This movement was confirmed in 1963 when 12 fin-clipped individuals were caught that had been marked as emigrants from Eagle Creek in the fall of 1962. In 1964, 2.7 percent of the fish captured from this July migration were fall chinook salmon that had been previously tagged and released in the upper reservoir.

According to Durkin et al. (1970), this upstream movement of fish into the Snake River may be related to the environment of the reservoir. The reservoir was rapidly filled early in the 1963 season, and, except for a minor drawdown of 3 m. in May, it was at full pool. Some Eagle Creek fish moved up the reservoir in 1963, possibly because surface currents frequently moved toward the upstream end of the reservoir. Late arrivals may have been attracted upriver by the relatively cooler, oxygenated water as the smolting phenomenon (Hoar, 1963; Conte, Wagner, Fessler, and Gnose, 1966) attenuated and reservoir temperature and oxygen conditions deteriorated (Ebel and Koski, 1968). As the river temperature increased to 20° C., the fish returned to the reservoir. In 1964, when the surface level of the reservoir was lower, Eagle Creek fish were not captured in the Snake River; however, recovery of fall chinook salmon that had been marked and released in the upper reservoir again suggested an upstream response to cooler water.

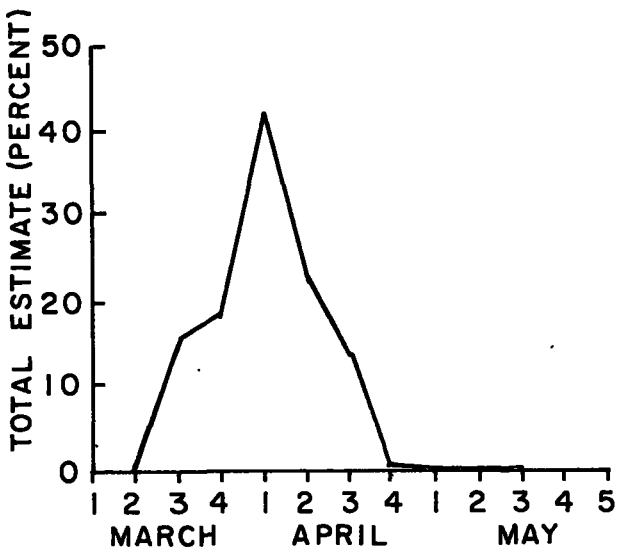

FIGURE 12.—Timing of migration of juvenile hatchery-reared sockeye salmon from the Snake River to Brownlee Reservoir, 1965.

ESTIMATES OF IMMIGRATION

Recruitments by age-group and population were estimated each year from data on release and recapture of marked fish. Estimated recruitment (N) was obtained by dividing the recaptures of marked fish (R) into the number of marked fish released (M) and multiplying by the catch (C).

In 1962, personnel of the Idaho Department of Fish and Game working upstream from the Bureau's migrant-dipper trap marked fall chinook juveniles and released them in the Snake River. These marked fish were used for the 1962 estimate. The marked fish group far exceeded the total catch of the migrant dipper. As a result, a single estimate was made for the Snake River population over the entire season. The 1962 estimate of recruitment for Weiser River chinook salmon was based upon the total catch by the scoop traps of the Idaho Department of Fish and Game and the estimated efficiency of these traps.

In 1963–65, the Snake and Weiser River fish that passed our trap were estimated each week and the values summed to yield the estimated total immigration. Fish for marking were obtained from the migrant dipper catches.

It was sometimes necessary to supply information by extrapolation when reliable data were lacking. When data on catch, recovery of marked fish, or marked fish released were unreliable or lacking, reliable data for 1 or 2 weeks preceding, bracketing, or following were used to supply an approximation of the needed data.

Studies on fish distribution in the Snake River in 1964 indicated that fingerling salmon were more concentrated near the surface during the day than at night (Monan, McConnell, Pugh, and Smith, 1969). Moreover, the increased length of louver leads in 1965 accentuated the difference between the percentage of the migration captured by the traps by day and by night. This difference necessitated the use of two catch figures in estimating the 1965 recruitments. Table 9 shows yearly differences in the ability of the migrant dipper traps to capture fish during the peak of migration.

SNAKE AND WEISER RIVERS

The number of juvenile native chinook salmon that entered Brownlee Reservoir after 1962 decreased each year. One of the reasons was that the adult spawners were intercepted and diverted to hatcheries downstream from Brownlee Dam. Our highest estimate of recruitment was in 1962 when 529,000 young chinook salmon entered from the Snake River (table 10); these fish were offspring of adults that had been transported past the dam and spawned in the fall of 1961. The highest number of juvenile chinook salmon from Weiser River (122,500) was also in 1962; these fish were offspring of spring migrants that had spawned in 1960.

The number of kokanee increased each year; nearly one-half million entered the reservoir in 1965.

Of the hatchery-reared fish released in the Snake River, sockeye salmon had the highest survival to

TABLE 9.—*Ability of migrant dipper traps to capture juvenile salmon during peak migration from the Snake River into Brownlee Reservoir, 1962–65*

Year of migration	Chinook		Coho [1]	Sockeye [1]	Kokanee [1]
	0	I			
	Percent	*Percent*	*Percent*	*Percent*	*Percent*
1962	2.36	[5]	[4]	[4]	[4]
1963	3.56	16.70	[4]	[4]	[5]
1964	8.13	16.85	13.46	[4]	6.2
1965 a.m. [3]	5.97	[4]	[4]	9.17	6.31
1965 p.m. [3]	2.35	[4]	[4]	7.10	1.10

[1] All age-group I.
[2] 6:00 a.m.–6:00 p.m.
[3] 6:00 p.m.–6:00 a.m.
[4] Not present in migration.
[5] Not tested.

TABLE 10.—*Estimates of juvenile salmon that entered Brownlee Reservoir from the Snake River system, 1962–65*

Year	Native species			Hatchery-reared species		
	Fall chinook	Spring chinook	Kokanee	Fall chinook	Coho	Sockeye
	Number					
1962 [1]	529,000	122,500	(2)	(3)	(3)	(3)
1963	374,000	15,000	500	(3)	(3)	(3)
1964	(2)	6,800	5,500	111,500	69,000	(3)
1965	(2)	3,200	506,800	162,800	(3)	360,000

[1] Calculated from data supplied in part by Idaho Fish and Game Department.
[2] Negligible numbers.
[3] Not present in migration.

the reservoir, and coho salmon the lowest. Survivals from release point to reservoir were inversely correlated with time spent in the river but not to distance traveled (table 11).

TABLE 11.—*Time in river and survival of hatchery fish from release site to Brownlee Reservoir, 1964 and 1965*

Year and distance	Species of salmon	Median release time	Migration peak	Time in river	Released	Estimate of fish passing collection facilities	Survival
				Weeks	*Number*	*Number*	*Percent*
1964 120 km	Coho	Mar. 23	Mid-May	7	375,000	69,000	18.4
	Chinook	Apr. 1	Mid-May	6	250,000	111,500	44.6
1965 88 km	Chinook	Mar. 20	Mid-May	7	592,000	162,800	27.5
	Sockeye	Mar. 27	Early April.	2	473,000	360,000	76.1

EAGLE CREEK

Estimates of migration from Eagle Creek were based on average efficiencies of the louver facility throughout the year (table 12). In 1962, the average efficiency was 10.2 percent but the louver was selective for larger fish. Alteration of the structure in 1963 increased the efficiency to 57.5 percent and eliminated selectivity. Straightening of the river channel above the louver in 1964 provided a straighter angle of approach for the current and further increased the efficiency of the louvers to 91.3 percent during the fall migration. In the spring of 1965, efficiency was less (85.2 percent) as a result of ice and high flows, which created currents that varied in velocity and direction of approach across the face of the louver.

Juvenile fish that entered the reservoir from Eagle Creek in 1962–63 (table 13) were progeny of native adults that were transported around Brownlee Dam in 1960–62. Thereafter natural production in the creek declined markedly because the policy of passing fish changed. Juvenile migrants in 1964–65 were primarily from adults that were surplus to hatchery needs and were transported from a collection facility at Oxbow Dam (19 km. downstream from Brownlee Dam) to holding ponds near the spawning area. Prespawning fish were held in these ponds until nearly mature and then released into Eagle Creek.

TABLE 12.—*Collection efficiencies of the louver system at Eagle Creek, 1962–65*

Year	Efficiency of collection by period of migration	
	Spring	Fall
	Percent	*Percent*
1962		10.2
1963	14.7	57.5
1964	42.0	91.3
1965	85.2	(1)

[1] Not in operation.

TABLE 13.—*Estimates of juvenile spring chinook salmon that entered Brownlee Reservoir from Eagle Creek, 1962–65*

Year of migration	Estimated recruitment by season and age-group					Total
	Spring migration			Fall migration		
	0	I	II	0	I	
1962	(1)	(1)	(1)	116,000	1,200	117,200
1963	600	13,500	(2)	7,500	(2)	22,300
1964	(2)	6,700	(2)	(2)	(2)	7,200
1965	(2)	(2)	(2)	(1)	(1)	

[1] Not in operation. [2] Negligible numbers.

SUMMARY AND CONCLUSIONS

Movements of juvenile salmon and rainbow trout from tributary streams into Brownlee Reservoir were examined in 1962–65 as part of a study on the effect of a large impoundment on the migration and survival of anadromous fish. Estimated numbers of migrant juvenile salmon were determined by sampling of juvenile fish populations that were en route to the reservoir from the Snake and Weiser Rivers and Eagle Creek, the three tributaries supporting indigenous populations of salmon and anadromous rainbow trout. Juvenile fall and spring chinook salmon, kokanee salmon, and rainbow trout entered the upper reservoir via the Snake River. Hatchery-reared fall

chinook and coho salmon were released in the Snake River in 1964 and fall chinook and sockeye salmon in 1965. Migrations from Eagle Creek near the lower end of the reservoir included native spring chinook salmon and rainbow trout.

Progeny of spring chinook salmon from the Weiser River were fish of age-group I that ranged from 94 to 165 mm. long. This migration began before but partially overlapped a migration of fall chinook juveniles from the Snake River. The migration usually peaked in late April and early May. Estimated numbers of fish were: 1962—122,500; 1963—15,000; 1964—6,800; and 1965—3,200.

The migration of juvenile fall chinook salmon (age-group O) from the Snake River began in mid-April, peaked in mid-May, and was almost complete by mid-June. The fish were 33 to 103 mm. long. Estimated recruitments to Brownlee Reservoir in 1962 and 1963 were 529,000 and 374,000. Because few fish were passed above Brownlee Dam after 1962, migrations of wild fish in 1964–65 were negligible.

Migrant salmon from Eagle Creek were of wild populations of spring chinook salmon. The principal migration of juvenile chinook salmon (age-group 0; 53–125 mm.) was in the fall as irrigation decreased and water flows correspondingly increased. Temperatures ranged from 0° to 13° C. A lesser migration of age-groups 0, I, and II (45–168 mm.) occurred in the spring. Estimated recruitments from Eagle Creek were: 1962—117,200 (fall migration only); 1963—22,300; and 1964—7,200.

Native juvenile kokanee salmon (70–155 mm.) were observed in the Snake River each year in June and July, except in 1962. Their migrations were relatively short; most fish migrated in a 1-week period in late June or early July. Estimated recruitment of this species was 500 in 1963, 5,500 in 1964, and 506,800 in 1965.

Juvenile rainbow trout migrating from the Snake River and Eagle Creek were wild steelhead trout and wild and hatchery-reared rainbow trout. The Snake River populations (95–382 mm.) migrated in the spring from mid-March to late July, peaking from mid-April to mid-May. Juvenile trout, 52–285 mm. long, migrated from Eagle Creek in the fall and spring, but the principal movement coincided with high spring flows.

Juvenile fall chinook salmon, reared in a hatchery (age-group 0; 46–135 mm. long), were released in the Snake River above the reservoir during March and April, 1964–65. Some moved downstream past the trapping site within 3 days after release, but the migration peaked in mid-May, which was comparable to native migrations. The migration ended in late June in 1964 and in early July in 1965. Of 250,000 juvenile fall chinook salmon released in 1964, 111,500 were estimated to have entered the reservoir. In 1965, the estimated recruitment was 162,800 of the 592,000 fish released.

Hatchery-reared coho salmon yearlings (71–166 mm.) released in middle to late March 1964, migrated slowly; they appeared at the trap site 4 weeks after the first release, peaked during the first week of May, and continued to migrate until mid-June. Of the 375,000 coho salmon released, 69,000 entered the reservoir.

Hatchery-reared sockeye salmon (86–175 mm.) appeared at the Snake River trap 2 days after their release in mid-March; the migration peaked in the first week of April and was complete by the end of April. An estimated 360,000 of 473,000 fish released entered the reservoir.

Survival to the reservoir of hatchery-reared salmon varied inversely with time spent in the Snake River but was not related to distance of planting site above Brownlee Reservoir.

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DISTRIBUTION AND MOVEMENT OF JUVENILE SALMON IN BROWNLEE RESERVOIR, 1962–65

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ABSTRACT

Juvenile salmon—chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), and sockeye and kokanee (*O. nerka*)—were studied. Their rates and direction of movement, spatial distribution, and successful passage to the outlet varied in relation to surface currents, water temperature, and dissolved oxygen concentrations.

Some juvenile salmon stayed in Brownlee Reservoir through the summer, fall, and early winter; the percentage varied between years. The percentages were highest in years with high water level and retarded, disoriented flows during the spring migration. Salmon that held over eventually concentrated in rather restricted areas of the reservoir through the summer and early fall, owing to high epilimnion temperatures and to low concentrations of dissolved oxygen that extended into the epilimnion from the hypolimnion.

When the water level was low and reservoir currents were oriented downstream, loss of orientation by juvenile salmon was least and movement through the reservoir was most rapid. These reservoir conditions varied, but salmon populations that migrated early in the year were most likely to encounter them.

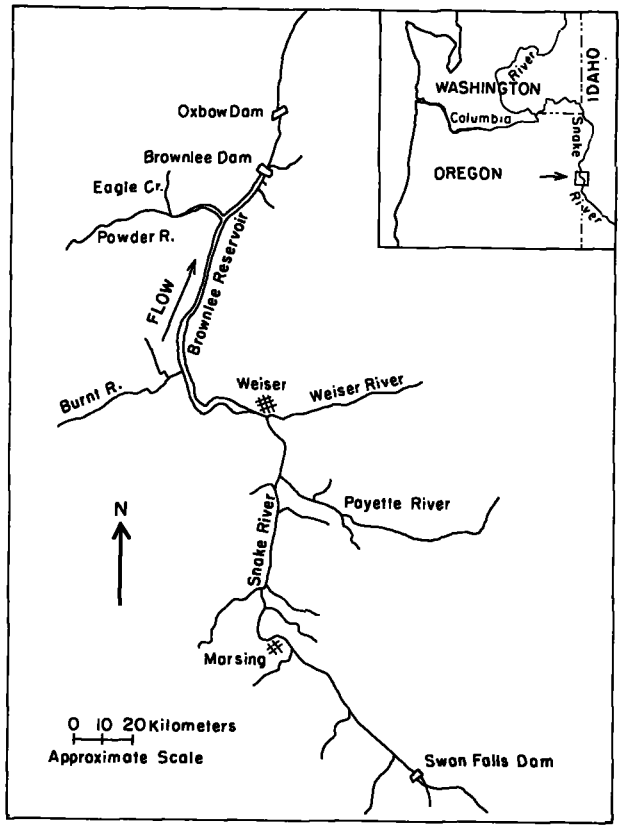

FIGURE 1.—Brownlee Reservoir, Snake River, and major tributaries.

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The completion in 1958 of Brownlee Dam on the middle Snake River (Soule, Heikes, Mitchell, and Schaufelberger, 1959) created a long, narrow reservoir along the path of migrating Pacific salmon (genus *Oncorhynchus*) and anadromous rainbow trout (steelhead) *Salmo gairdneri* (fig. 1). At full pool the impoundment is 92 km. long, less than 0.8 km. wide, and nearly 92 m. deep. The upper 24-km. of the reservoir is relatively shallow, slow moving, and forms a river-run impoundment. The lower 68 km., which thermally stratifies, lies within an arid mountainous terrain. Powder River Arm, a prominent appendage on the Oregon side, joins the reservoir 17 km. above the dam and extends westward for 15 km. The upper 5 km. of the arm forms a wide, shallow, unstratified pond when the reservoir is full. Juvenile salmon enter the reservoir from the Snake and Powder Rivers en route to the sea.

When Brownlee Reservoir was completed, detailed knowledge was lacking on the passage of Pacific salmon and steelhead trout through large reservoirs; therefore, BCF (Bureau of Commercial Fisheries) conducted detailed research at Brownlee in 1962–65. These studies covered native stocks of steelhead trout, spring and fall chinook salmon (*O. tshawytscha*), and kokanee (landlocked sockeye salmon, *O. nerka*) in addition to

hatchery-reared fall chinook, sockeye, and coho (*O. kisutch*) salmon. The research, which began in the spring of 1962, consisted of five studies: (1) limnology of the reservoir system (Ebel and Koski, 1968), (2) upstream migration of adult chinook salmon through the reservoir (Trefethen and Sutherland, 1968), (3) migration of juvenile salmon and trout into the reservoir (Krcma and Raleigh, 1970), (4) distribution and movement of juvenile salmon in the reservoir (this report), and (5) migration of juvenile salmon and trout from the reservoir (Sims, 1970).

Our report gives an account of movements and distributions of the juvenile salmon in relation to their environment. Data on the movements of juvenile steelhead trout were difficult to analyze and report, as we were unable to clearly distinguish them from the nonanadromous wild and hatchery-reared rainbow trout that were also in the reservoir.

EQUIPMENT AND PROCEDURES

To obtain the desired information, it was necessary to sample the juvenile fish in the lower 68 km. of the reservoir. This sampling involved both gear and marking efforts.

FISHING EQUIPMENT

Studies had indicated that four types of fishing equipment were needed to capture juvenile fish: floating traps, gill nets, purse seines, and two-boat trawls. These, together with the fingerling collection facility (skimmer net) of the Idaho Power Company 1.5 km. above the dam, provided basic data on the movement of juvenile salmon within the reservoir. The sampling equipment was deployed to intercept migrants in the upper, middle, and lower reservoir from early in the year until late fall (fig. 2).

Floating Traps

Floating traps were the most effective fishing gear for capturing age-group 0 salmon (fig. 3). The dimensions of the trap, mesh size, and fishing methods were similar to those described by Rothfus, Erho, Hamilton, and Remington.[1] From one to seven of these units were used. The traps were tended every other day early in the year and each day between mid-March and early July. Thereafter, as fish became less available, the traps were operated with diminishing frequency and in most years were removed by late July.

Gill Nets

The number of gill net stations fished depended on the water level and its effect on the length of the reservoir. At each site, two or three parallel sections of multifilament net, 30 m. long by 4.5 m. deep, were fished at predetermined depths in a manner similar to that described by Rees (1957). The mesh sizes were 1.9, 2.5, 3.1, 3.8, 5.1, and 6.3 cm. stretched mesh, of which the 2.5- to 3.8-cm. sizes were most effective. The nets were most efficient on salmon over 90 mm. fork length and at night.

Purse Seines

Two purse seines (Durkin and Park, 1967) were used as mobile sampling gear on fish concentrations throughout the limnetic environment of the reservoir. One of the seines was 180 m. long and 10.5 m. deep; the other was 210 m. long and 16.5 deep. Both were set from a barge. Purse seines were used in the main reservoir during spring and early summer and in the Powder River Arm during fall.

Two-Boat Trawls

Surface trawls (Johnson, 1956) were used to locate concentrations of salmon and to determine their relative abundance. The trawls were 3.0 m. high, 5.4 m. wide at the mouth, and 7.8 m. long.

MARKING

Various types of marks were placed on captured juvenile fish for identification at recapture. The type of mark depended on the size of fish. Fish less than 100 mm. long were marked with vinyl thread tags (developed by personnel of the Fish Commission of Oregon). A jaw tag clamped to the left mandible marked the fish (100 to 250 mm. long); fish over 250 mm. had a plastic dart tag. Color coded tattoos, used in 1962, were discontinued when the vinyl thread tag became available. Other groups of fish were marked by clipping fins before they entered the reservoir (Krcma and Raleigh, 1970).

[1] Lloyd O. Rothfus, Michael Erho, J. A. R. Hamilton, and Jack D. Remington. 1964. A study of reservoir rearing of coho salmon in Lake Merwin, Washington. State Wash. Dep. Fish., Res. Div., 18 pp. (Processed.)

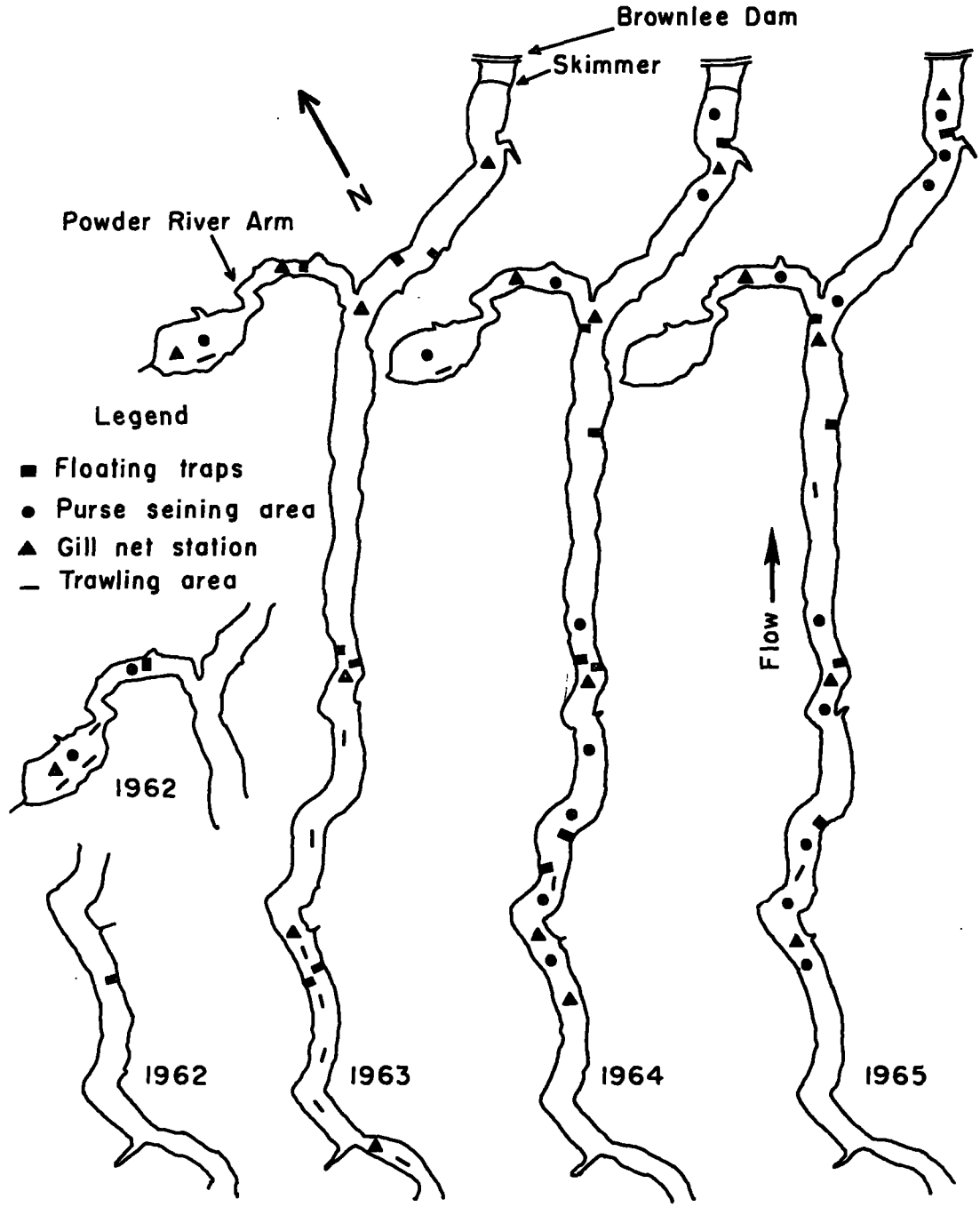

FIGURE 2.—Location of sampling areas and types of fishing gear used in Brownlee Reservoir, 1962–65.

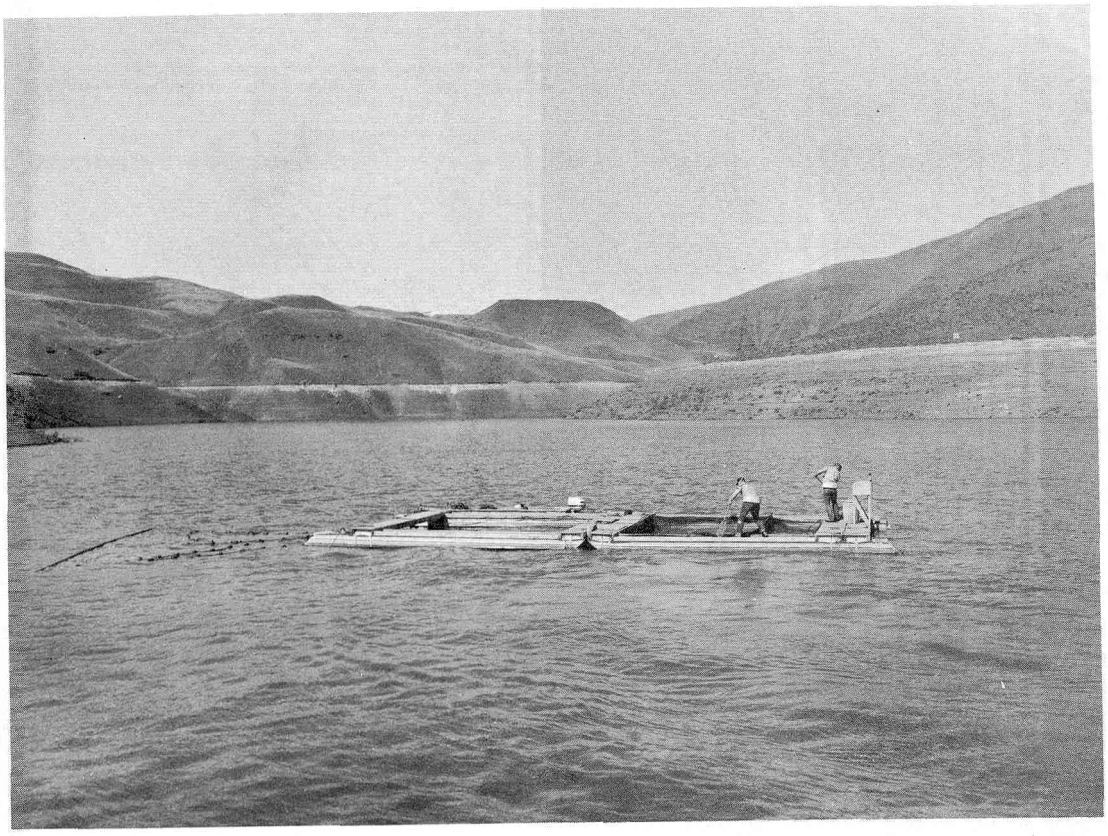

FIGURE 3.—Floating trap used to capture juvenile salmon moving near the shore. Salmon were diverted to the trap by a lead extending from the shoreline.

A combination of length-frequency ranges and the above marks identified specific populations and individual fish and, thus, yielded data on direction and rate of movement, spatial distribution, growth, and survival of the populations of salmon that entered the reservoir.

Upon capture, the fish were anesthetized, measured (fork length) to the nearest millimeter, examined for marks, and tagged if not previously marked. Scales for age determination were taken each month from a sample of up to 10 fish in each 5-mm. length group in the catches. All fish were released near the capture site.

THE ENVIRONMENT OF THE RESERVOIR

Apparently, the conditions exerting the greatest effect on the environment of Brownlee Reservoir were the size and timing of the annual reservoir drawdown and fillup and the volume of flow through the impoundment. Water level of the reservoir, filling, spillway discharge, and flow varied considerably during the 4-year study (fig. 4). The drawdown was least (6.4 m.) in 1963 and greatest (28.3 m.) in 1965. Drawdown typically began in December or January. Filling began each year in early April except in 1965 when it was delayed until mid-May. Filling was nearly complete by late June 1962, mid-April 1963, mid-June 1964, and mid-June 1965. The extent of drawdown or fill determined the length of the reservoir, and the time of filling determined the quality of the water through which the fish migrated.

SURFACE CURRENTS

The volume of inflow and outflow, together with the water level of the reservoir, determined the orientation and stability of currents and the velocity of flow. Figure 5 shows typical currents under different reservoir conditions.

The stability, velocity, and orientation of the reservoir surface currents varied considerably over the study years (1962–65). Surface currents near

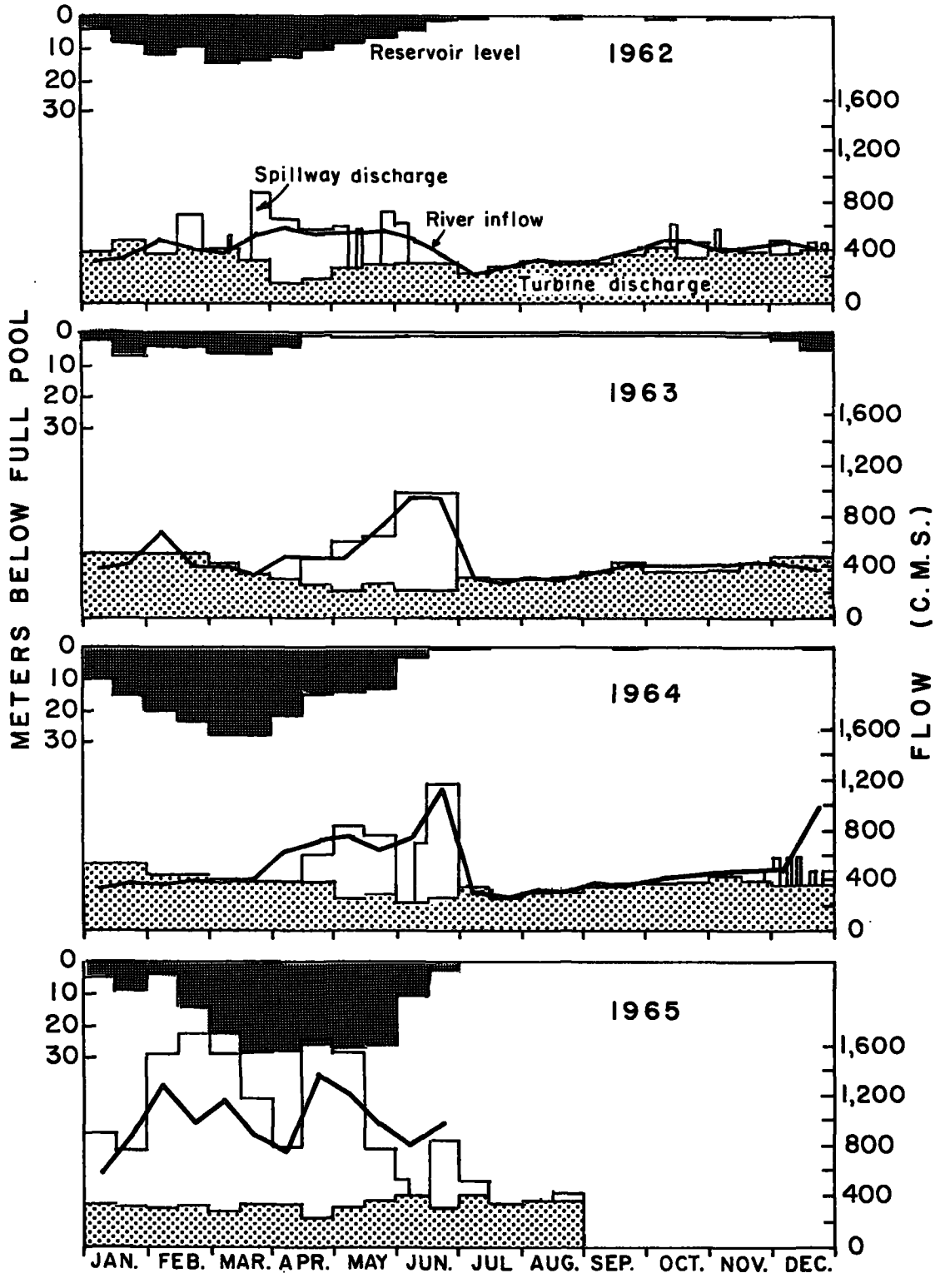

FIGURE 4.—Semimonthly averages of reservoir water level, turbine and spillway discharges, and Snake River flow into Brownlee Reservoir, 1962–65. Flow is in cubic meters per second.

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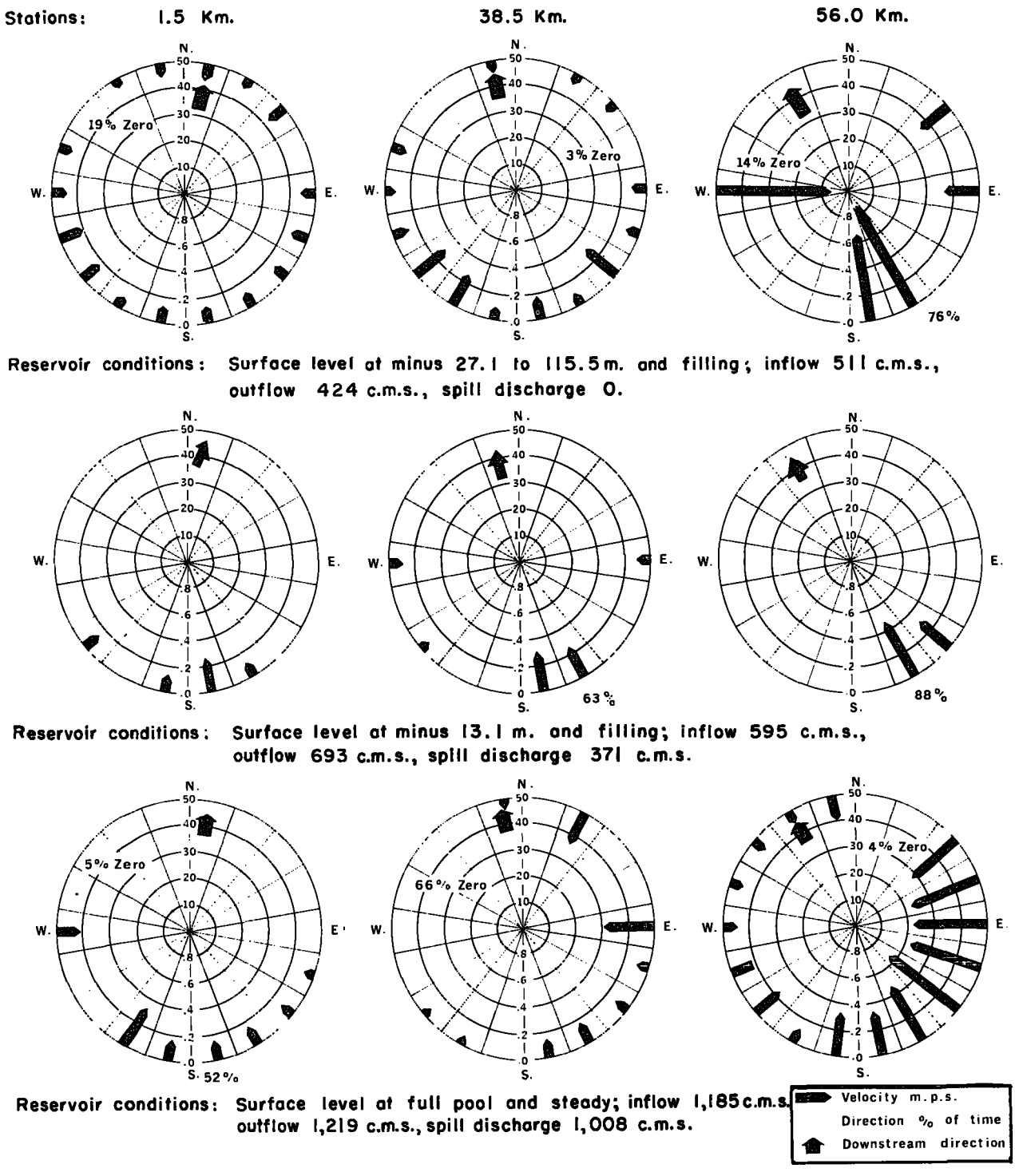

FIGURE 5.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s. scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir. Direction of current reads toward point of wedge. Percentages of time (if any) during which no flow was detectable are given within each circle; when flow was in a particular direction more than 50 percent of the time the percentage is given outside of the circle. Adapted from Ebel and Koski (1968).

the dam were affected mainly by the presence or absence of spillway discharges even when the reservoir level was down 27.1 to 15.5 m. (fig. 5). Surface currents in the middle and upper sections of the reservoir, however, appear to be little affected by spillway discharges. Reservoir level and volumes of flow had the greatest effect on the orientation and stability of the surface currents in these areas (fig. 5).

TEMPERATURE CYCLE

The volume of flow and water level of the reservoir also influenced the characteristics of temperature and oxygen in the impoundment. Figure 6 shows a generalized annual thermal cycle in the reservoir. From January to mid-March, isotherms of 1° to 6° C. were vertically aligned. Horizontal alignment of isotherms began in late March, and thermal stratification developed by early June. A sharp convergence line (not shown in fig. 6) was formed in the upper reservoir in late spring of 1963 when cold, dense river water sank below the warmer surface water (Ebel and Koski, 1968). In late June, the temperatures of the river water and surface water were similar and the line disappeared. By mid-July the entire reservoir was usually stratified with well-defined epilimnion, thermocline, and hypolimnion. In late summer, water temperatures ranged from 5° C. in the hypolimnion to as high as 24° C. at the surface. In mid-October a convergence line was again formed by rapidly cooling water from the Snake River and the thermocline was gradually eroded. Vertical alignment of isotherms began again in early December.

DISSOLVED OXYGEN CYCLE

The dissolved oxygen content of the reservoir followed a similar cycle each year (fig. 7). The reservoir was near saturation and relatively stable from January to mid-March, at which time oxygen concentrations began to decline in the deeper parts. Depletion of oxygen continued through the summer until August when all water below 30 m. had less than 3 p.p.m. In September, the cooler, oxygenated water from Snake River began to sink below the surface of the upper reservoir. By November, most of the water had 7 to 9 p.p.m. of oxygen.

These seasonal changes occurred each year, but with certain differences. In 1965, a drawdown of 28.3 m. and a late filling period caused: (1) late formation of a thermocline, (2) higher average temperatures from top to bottom, (3) lower oxygen concentrations during August and September, and (4) currents that were consistently oriented downreservoir through May. Drawdown was significant in 1964 (26.7 m.), but the filling began earlier and volumes of inflow and outflow were smaller. Temperatures were lower and concentrations of dissolved oxygen were higher in 1964 than in 1965, but conditions were less favorable for fish than in 1962 or 1963. A reservoir drawdown sufficient to allow sustained downreservoir current velocities can prevent a sharply defined convergence line from forming. For this reason, no convergence line formed in the upper reservoir in the spring of 1962, 1964, or 1965.

Generally, the temperatures and dissolved oxygen in the reservoir were within acceptable limits for survival of salmon during their spring migration (March-June). These conditions, however, began to deteriorate by late June and were marginal to restrictive until late September. A more detailed report of the environment was presented by Ebel and Koski (1968).

DISTRIBUTION AND MOVEMENT OF NATIVE STOCKS OF SALMON

Juvenile salmon from four populations were indigenous to Brownlee Reservoir: Two were progeny of spring chinook salmon, one of fall chinook salmon, and one of kokanee. The account of movement and behavior of juvenile salmon while passing through the reservoir environment is presented by species and population.

SPRING CHINOOK SALMON

Offspring of spring chinook salmon enter the reservoir from two areas: the Weiser River, a tributary of the Snake River, and Eagle Creek, a tributary of the Powder River (fig. 1). Migrants from Weiser River must traverse the entire reservoir on their seaward migration, whereas Eagle Creek migrants have less than one-half of the reservoir to negotiate. The two populations also differ in average age, size, and season of entry. Table 1 gives yearly estimates of the numbers of young fish that entered the reservoir in 1962–65.

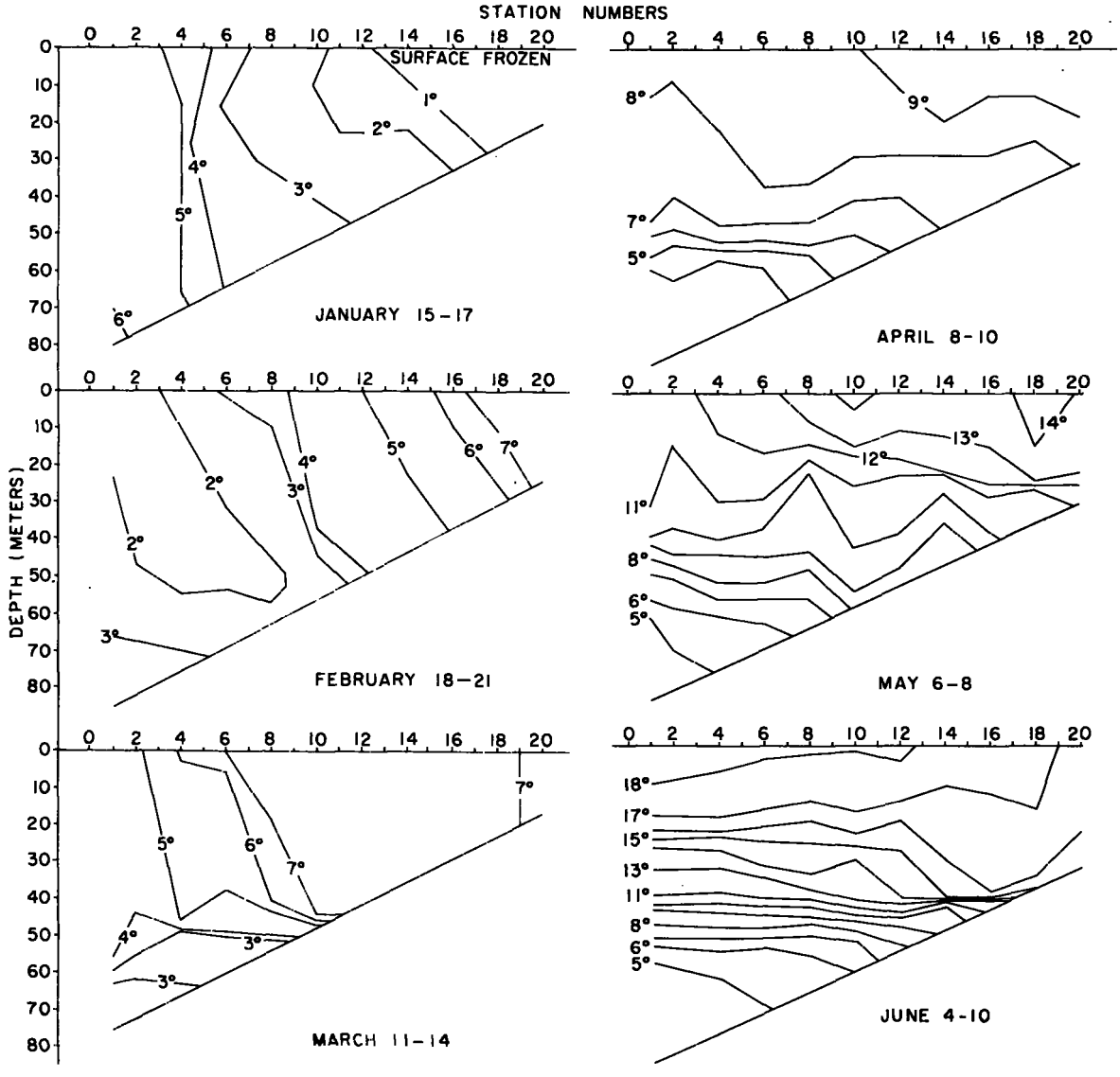

FIGURE 6.—Water temperature profile and stratification cycle at Brownlee Reservoir, 1963, modified from Ebel and Koski (1968).

TABLE 1.—*Estimated numbers of juvenile spring chinook salmon that entered Brownlee Reservoir, 1962–65 (from Krcma and Raleigh, 1970)*

Year	Weiser River origin	Eagle Creek origin				
	Age-group I	Spring migrants			Fall migrants	
		Age-group			Age-group	
		0	I	II	0	I
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
1962	122,500	(1)	(1)	(1)	116,000	1,200
1963	15,000	600	13,500	(2)	7,500	(2)
1964	6,800	(2)	6,700	(2)	(2)	(1)
1965	3,200	(2)	(2)	(2)	(1)	(1)

[1] Not estimated.
[2] Negligible numbers.

Weiser River Population

Spring chinook salmon from the Weiser River, 106 to 176 mm. long, entered the reservoir as yearlings from early April until late June. The migration peaked from late April to early May each year.

Through late May, spring chinook salmon from the Weiser River that were in the reservoir could be distinguished from fall chinook salmon of age-groups O and I on the basis of length; they were longer than age-group O but shorter than age-group I of the fall stock. After late May, as length

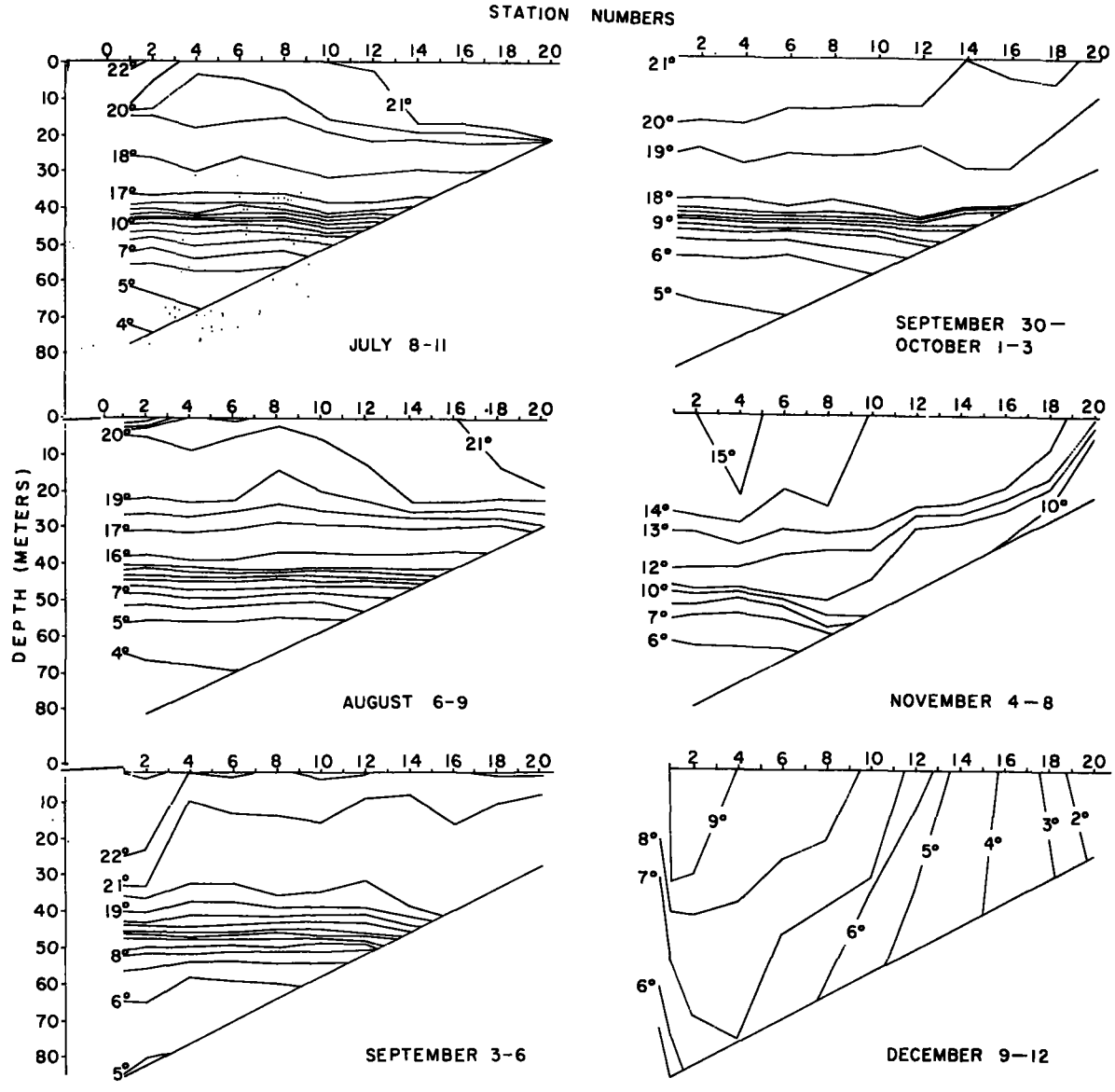

FIGURE 6.—Continued

measurements overlapped, the populations were separated on the basis of marked fish in the catch. By late May, however, the peak of migration from the Weiser River had usually passed through the reservoir.

A comparison of the timing of peak catches in the Snake River above the reservoir and at Brownlee Dam provided rough estimates of the time required for passage through the reservoir—about 2 weeks in 1962 and 3 weeks in 1963 (fig. 8). Differences in flow and length of reservoir between the 2 years appear to account for the more rapid movement in 1962. From early May through early June 1962 the reservoir was drawn down 9 m. and was about 75 km. long. Over the same period in 1963 it was nearly full and 92 km. long (fig. 4). Because of decreased depth and length in 1962, the average movement of the water mass through the reservoir was more rapid and conducive to passage of fish.

On the basis of the comparison of peak catches, the movement through the reservoir of yearling chinook salmon from the Weiser River averaged 6.4 km. per day in 1962 and 4.8 km. per day in 1963. Recapture of 334 marked individuals in 1962 and 1963 indicated that these fish moved through

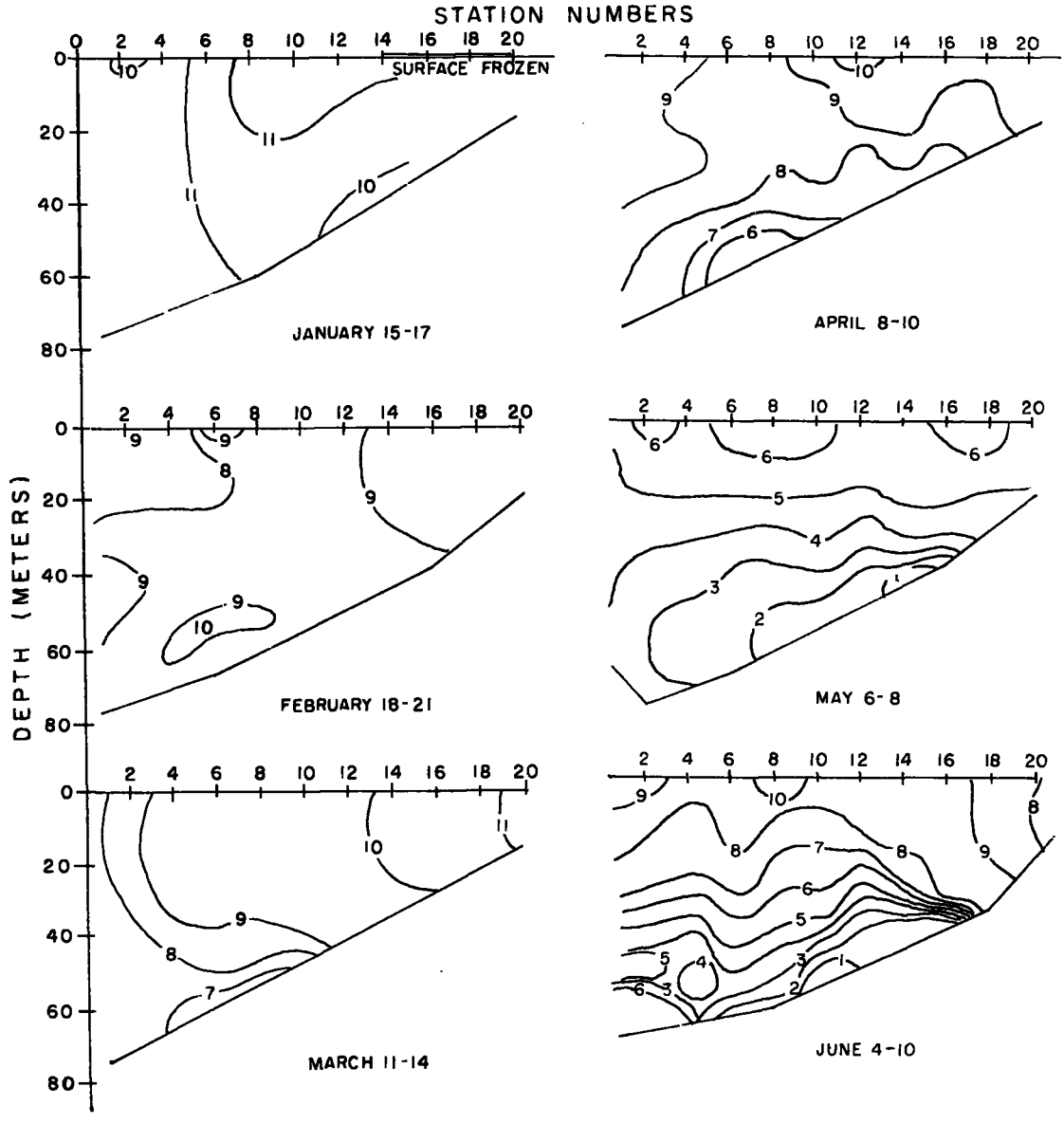

FIGURE 7.—Dissolved oxygen (p.p.m.) profiles from Brownlee Reservoir, 1963, modified from Ebel and Koski (1968).

the reservoir with little wandering and corroborated the estimated rates of movement.

In 1962, about 3,200 fish from the Weiser River population were marked as they were entering the reservoir. Six were recaptured the following spring (1963) in the reservoir. In 1963, about 1,900 fish were marked during their migration into the reservoir; in late June and July, 23 were recaptured in the Snake River. A study of growth patterns on their scales showed that they had returned upstream from the reservoir. These recaptures indicate that some fish of the Weiser River population become disoriented and hold over in the reservoir, but this behavior did not appear to be a major factor in the general movement of this early migrating population of large yearling fish.

In general, the Weiser River chinook salmon passed through a more benign environment in the reservoir than did populations migrating later in the season (figs. 6 and 7).

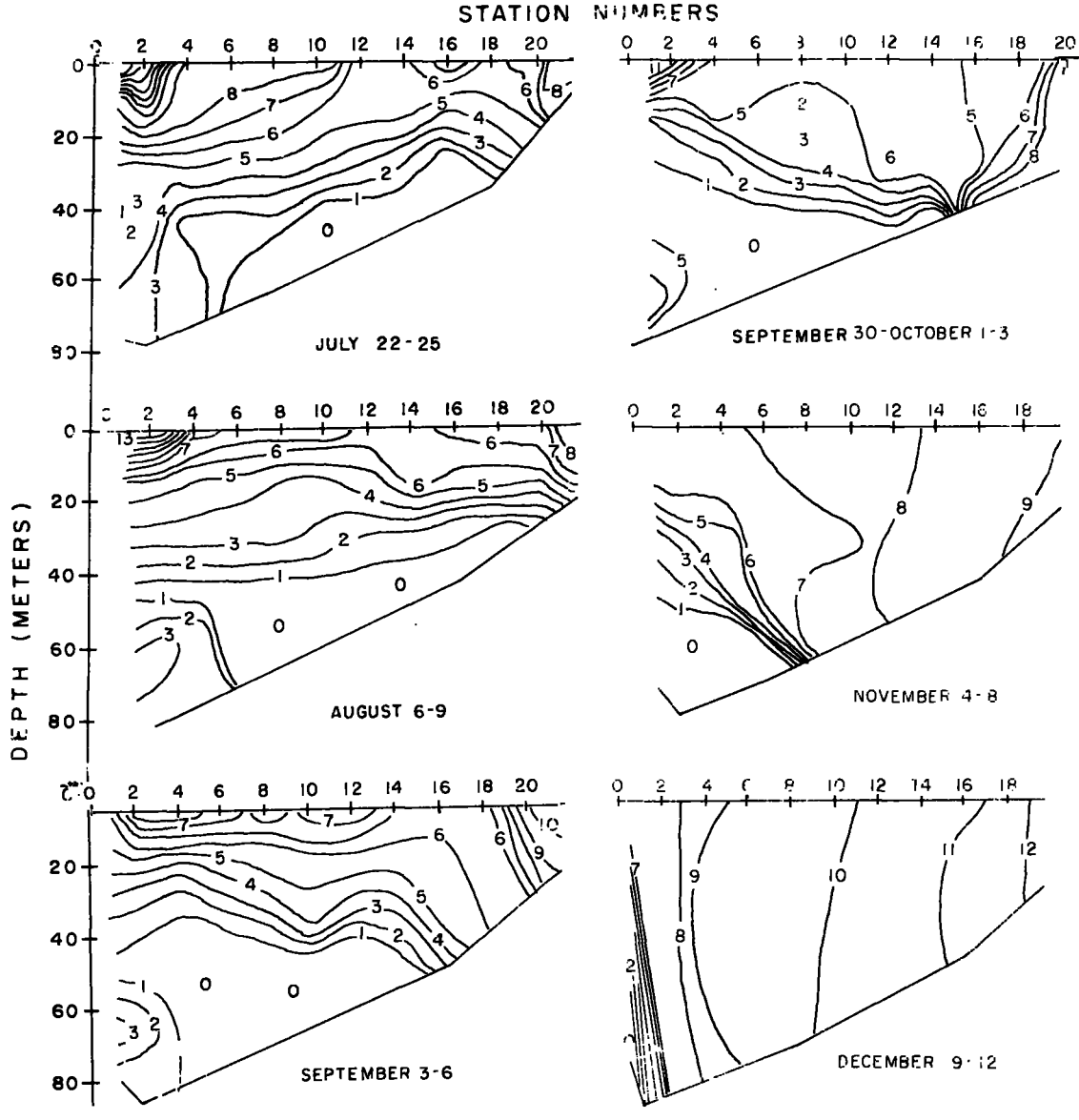

FIGURE 7.—Continued

Eagle Creek Population

The principal migration of spring chinook salmon from Eagle Creek into the reservoir was in the fall and consisted of age-group O fish, 53 to 125 mm. long. This movement was followed by a second lesser migration of age-group I fish, 65 to 138 mm. long, from February to May (Krcma and Raleigh, 1970). Only chinook salmon that had held over from the spring migrations were found in significant numbers in the reservoir at that time of year. These populations were separable by size (fig. 9).

Continuous recovery from the upper Powder River Arm and the main reservoir of marked age-group O fish from the fall migration from Eagle Creek indicated that not all these fingerlings continued to move through the reservoir. Further evidence was obtained by comparing mean lengths of fish caught leaving Eagle Creek with those of fish from the reservoir. Fish that remained in the stream grew little through the fall and winter, whereas those in the reservoir continued to grow.

Incidental movement of Eagle Creek fish from the reservoir began in November, but a sustained

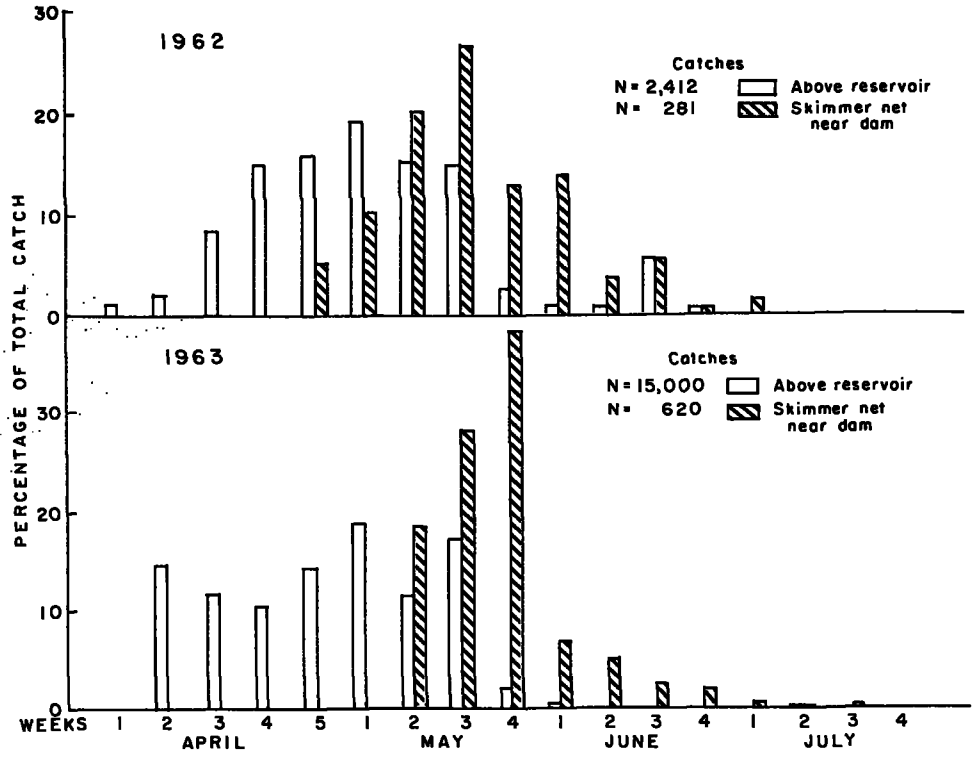

FIGURE 8.—Percentages of the total catch of juvenile spring chinook salmon from Weiser River, taken during different weeks at the upper and lower ends of Brownlee Reservoir, 1962–63.

outmigration did not occur until after the first of the year (Sims, 1970). There were two major migrations of Eagle Creek fish from the reservoir each year; the first consisted of fish that entered the reservoir in the fall and overwintered, and the second consisted of spring migrants that moved directly from the stream to the dam (fig. 10). The first group migrated from the reservoir primarily from late January to April and the second group from late March to June (fig. 11).

We investigated the possibility that the reservoir might be delaying the seaward migration of the fall migrants. Tagging data showed that most fall migrants spent about 3 months in the reservoir, whereas most spring migrants moved through the reservoir in a much shorter time. In 1964 and 1965, groups of Eagle Creek fall migrants were marked, transported around Brownlee and Oxbow Dams, and released in the Snake River. Sampling at Ice Harbor Dam (442 km. downstream from Brownlee) showed that fish released in the river below the dams overwintered in the Snake River and arrived at Ice Harbor Dam at about the same time as the group that passed through the reservoir.[3] It appears, therefore, that Brownlee Reservoir did not unduly delay the fall migration from Eagle Creek and that these fish normally overwinter before going to sea.

Although Brownlee Reservoir did not appear to cause an appreciable delay in the seaward migration of the fall migrants, some fish from Eagle Creek became disoriented in the reservoir under certain conditions. In 1962 and 1964, fish from Eagle Creek moved consistently downstream toward the dam. In 1963, however, a segment of the population moved upreservoir. This movement was proven by capture of 12 marked individuals in the Snake River 4 km. above the reservoir in late June and July 1963. Drawdown of the reservoir exceeded 14 m. in 1962 and 1964 but was only 6.4 m. in 1963. Figures 4 and 5 indicate that these conditions would provide weak downstream currents in 1962 and 1964 but disoriented currents in

[3] Personal communication, Howard Raymond, Fishery Biologist, BCF Biological Laboratory, Seattle, Wash., June 1965.

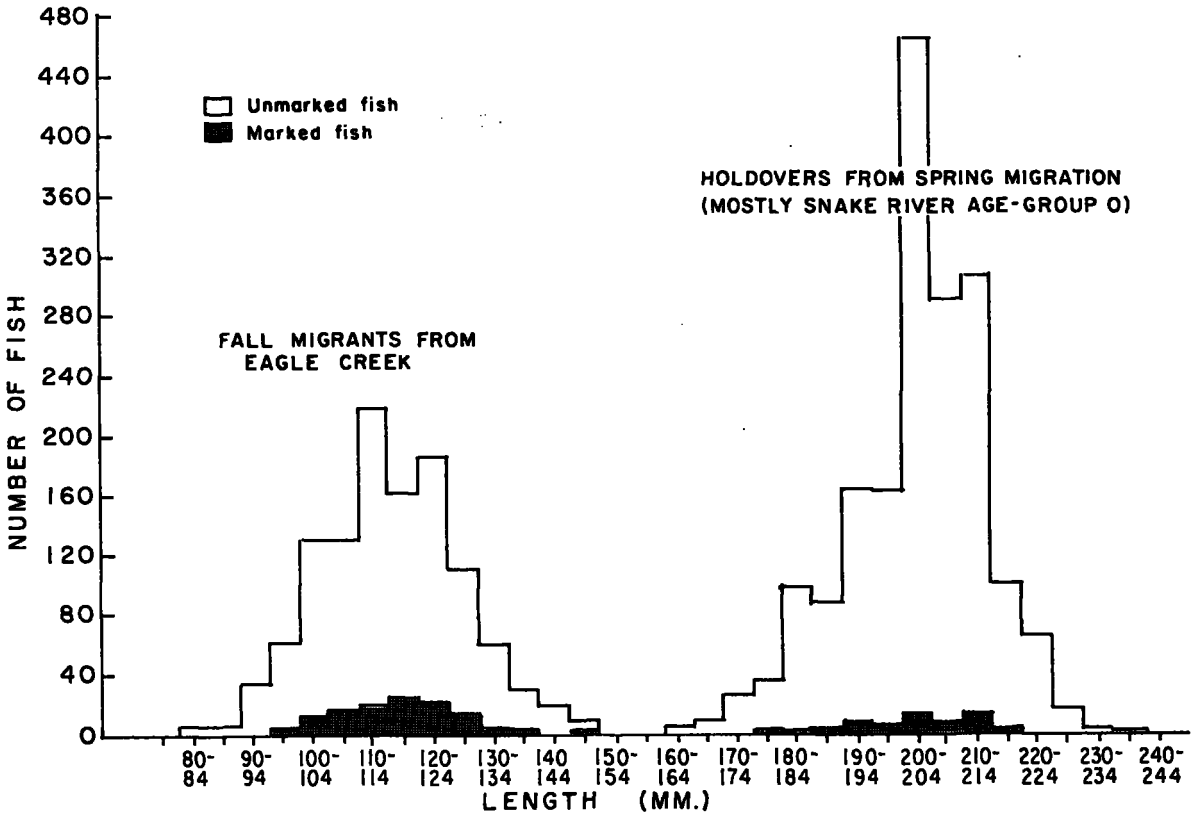

FIGURE 9.—Lengths of juvenile spring chinook salmon from Eagle Creek that entered Brownlee Reservoir in the fall and lengths of holdover chinook salmon from populations that entered in the spring, in samples collected September through December 1962.

1963. We presume that some Eagle Creek fish moved upreservoir in 1963 because of frequent upreservoir currents. The fish that arrived at the upper end of the reservoir in late June and July as the "smolting" condition (Hoar, 1963; Conte, Wagner, Fessler, and Gnose, 1966) was attenuating and reservoir temperature and oxygen conditions were deteriorating (figs. 6–7) may have been attracted upstream by the relatively cooler, oxygenated water of the Snake River.

FALL CHINOOK SALMON OF AGE-GROUP O

Juvenile fall chinook salmon entered the reservoir as age-group O and at a smaller length (33–105 mm.) than other populations. They began their migration from spawning grounds in the Snake River about 120 km. above the reservoir. Table 2 gives estimates of fall chinook juvenile salmon that entered the reservoir.

We studied the offspring of native populations in 1962 and 1963; hatchery-reared juvenile fish from other sources were released in the spawning area for study as they passed through the reservoir in 1964 and 1965.

TABLE 2.—*Estimated numbers of fall chinook salmon that entered Brownlee Reservoir, 1962–65 (from Krcma and Raleigh, 1970)*

Year	Native	Hatchery-reared
	Number of fish	
1962	529,000	(1)
1963	374,000	(1)
1964	(2)	111,500
1965	(2)	162,800

[1] None released.
[2] Negligible numbers.

Juvenile native fall chinook salmon entered the reservoir from late April through June in 1962 and from late April through mid-June in 1963. Mean lengths of age-group O fish in the reservoir were 56 to 85 mm. through the 1962 season and 75 to 195 mm. in 1963.

Peak catches above the reservoir and at the fingerling collection facility near Brownlee Dam

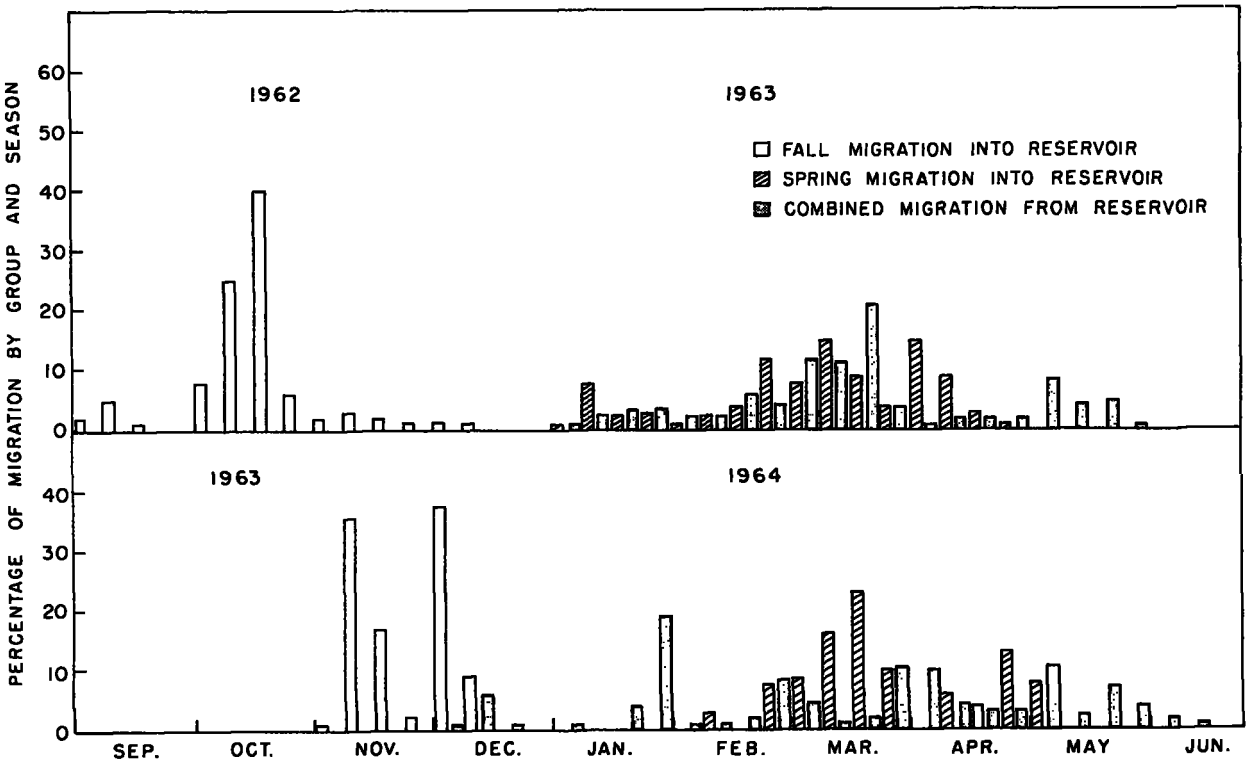

FIGURE 10.—Percentage of total catches of juvenile spring chinook salmon from Eagle Creek that entered and that left Brownlee Reservoir in different months, 1962–64. Fish entering the reservoir were caught in a louver trap at Eagle Creek (Krcma and Raleigh, 1970); fish leaving the reservoir were caught in skimmer net traps in the forebay (1963) or in scoop traps below the dam (1964).

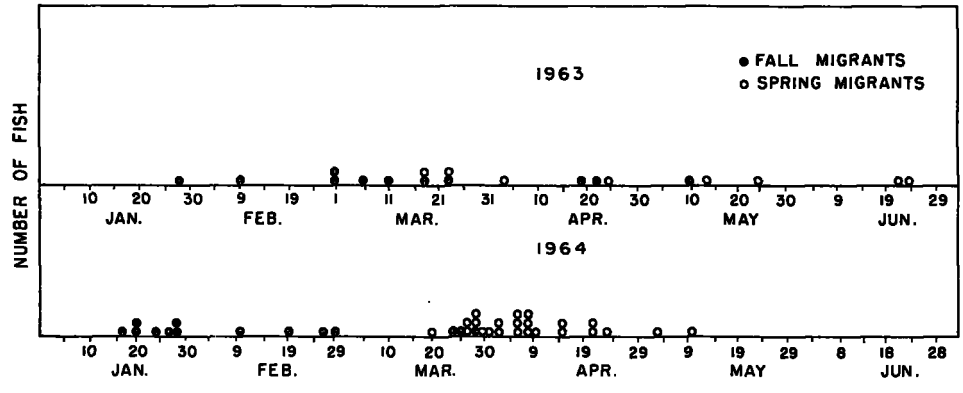

FIGURE 11.—Date of arrival at Brownlee Dam of juvenile spring chinook salmon tagged at Eagle Creek during the fall and spring migrations of 1962–64. Each circle represents one recovery.

showed that juvenile fall chinook salmon passed through the reservoir in about 2 weeks in 1962 and in about 7 weeks in 1963 (fig. 12). Figures 4 and 5 indicate that the currents would have been of low velocity but moderately well oriented downstream during the 1962 migration. In 1963, the migrant fall chinook salmon entered the reservoir a week later than in 1962 (fig. 12). At that time the reservoir was drawn down only 3 m. and was being filled. Although volumes of inflow and outflow were moderate to high, the currents were disoriented (figs. 4 and 5).

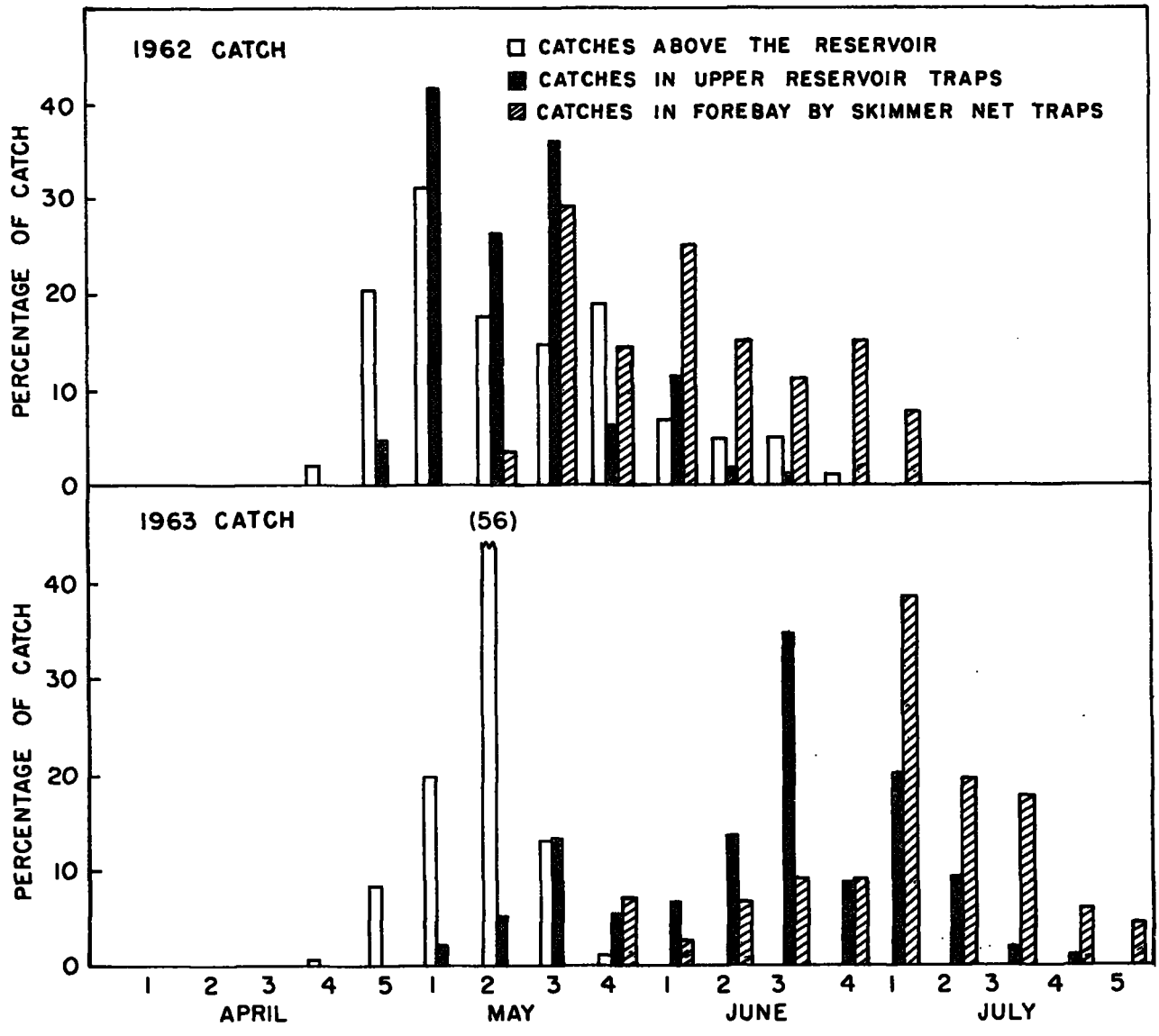

FIGURE 12.—Catches of native juvenile fall chinook salmon in the upper reservoir and at Brownlee Dam, 1962–63.

Trap and surface trawl catches in 1963 indicated that most of the migrants were remaining in the upper reservoir. They were in the Snake River water mass upstream from the point where the colder river water sank below the reservoir surface (Ebel and Koski, 1968; Raleigh and Ebel, 1967). Gill net sampling showed the fish were near the surface of the reservoir through mid-June. By late June, however, they were captured at all depths. At this time the river water began to warm and mix with the reservoir water mass; the convergence line disintegrated, and the juvenile fish began to move through the reservoir. Peak catches by traps in the upper reservoir and at Brownlee Dam showed that after the initial 5-week delay the fish migrated through the reservoir in about 2 weeks (fig. 12).

In 1963, the capture of a number of large fingerlings in the Snake River above the impoundment indicated a pronounced upreservoir movement of young fall chinook salmon (Krema and Raleigh, 1970). Growth patterns on the scales showed that these fish had lived in the reservoir. The identification of marked fish indicated that most of the fish that moved upstream had migrated from Eagle Creek and the Snake River in the spring of 1963.

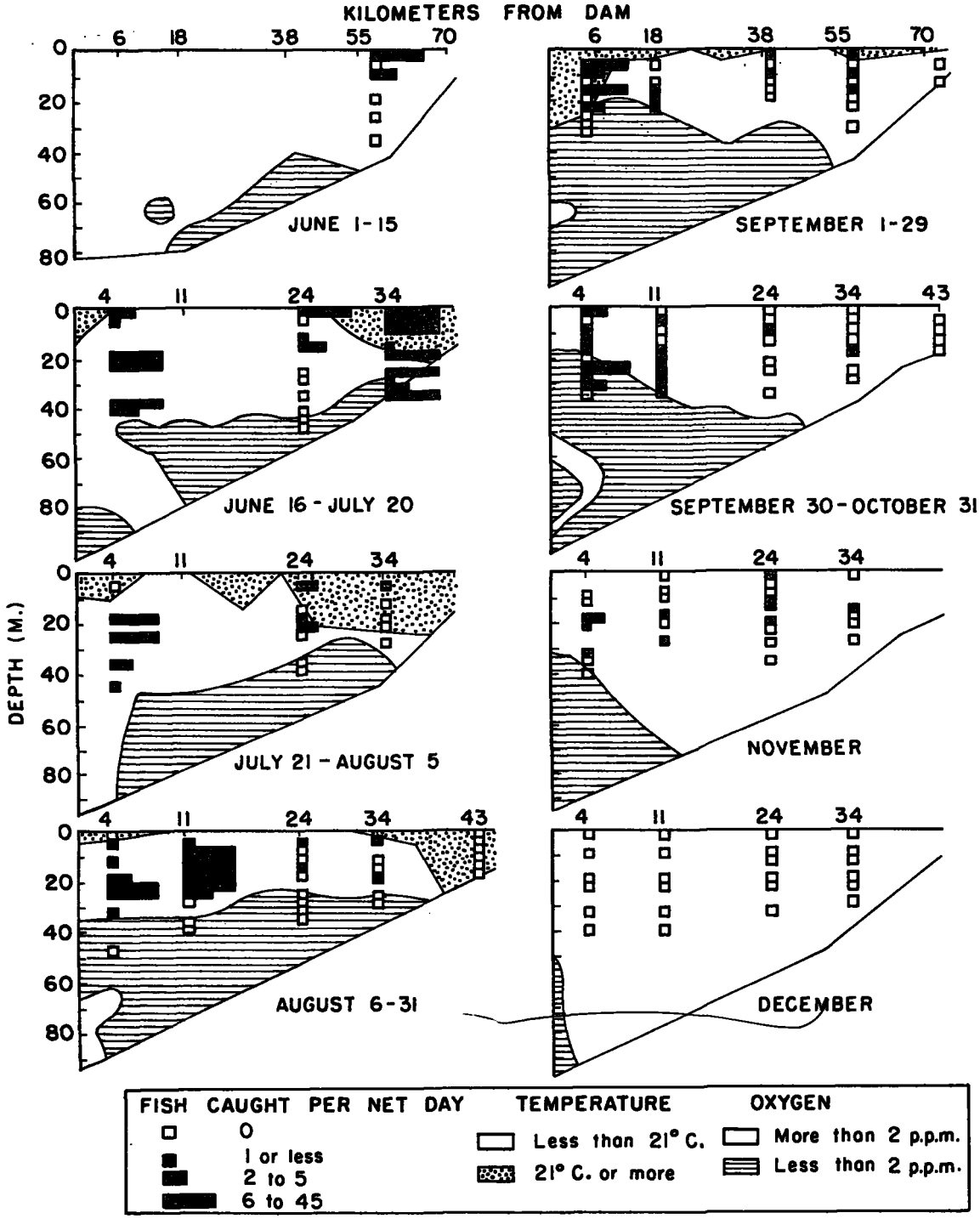

FIGURE 13.—Distribution of juvenile fall chinook salmon in Brownlee Reservoir in relation to critical oxygen and temperature regimes. Fish caught in gill nets in 1963.

We presume that these fish were attracted upstream by the cooler water of the Snake River (14–22° C.), which averaged 2 to 3° C. less than the reservoir. The subsequent downstream migration coincided with an increase in river temperatures to over 18° C. and the breakdown of the convergence line.

In most years, after the migration of smolts ended in late June or July, some chinook salmon remained in the reservoir as holdovers. In 1963, most of the migrants did not leave the reservoir even though the outmigration continued into August (Sims, 1970). The holdover fish were from all salmon populations but were mainly progeny of fall chinook salmon. They were easily distinguished from more recent arrivals by their large size; in addition, some had identifying fin clips or tags.

Gill net catches showed that the holdover salmon had a restricted spatial distribution through the summer and early fall. By late June or early July, surface temperatures exceeded 20° C. and oxygen depletion progressed upward from the bottom. These conditions were especially prevalent in the upper end of the reservoir (figs. 6 and 7). Increasing epilimnion temperatures and decreasing hypolimnion levels of dissolved oxygen eventually confined the holdovers into restricted areas unfavorable for juvenile salmon (fig. 13). By late September and October, conditions began to improve and the surviving juvenile salmon dispersed throughout the reservoir.

This same sequence of events occurred each year, but with modification. According to Raleigh and Ebel (1967), the amount of reservoir drawdown and the time and duration of the subsequent filling period appeared to be most significant in creating large differences in temperature and oxygen from year to year. In 1965, the large drawdown (28 m.) and prolonged filling (fig. 4) caused late formation of a thermocline, high temperatures, and low oxygen concentrations during late summer. In 1964, drawdown was significant (27 m.) but the filling period was shorter. Water temperatures and oxygen concentrations through the summer were more favorable than in 1965 but less favorable than in 1963, when the drawdown was small (3 m.) and the filling period was early and short.

Estimates of movement of juvenile fall chinook salmon into Brownlee Reservoir (Krcma and Raleigh, 1970) and later escapement (Sims, 1970) verified that the survival of holdover salmon was extremely poor. Fortunately, the conditions that brought about the harshest summer environment (large drawdown and delayed fill) were also the conditions that facilitated rapid passage of fingerlings through the impoundment (Ebel and Koski, 1968; Sims, 1970).

Holdovers of salmon were encountered in the Powder River Arm in October 1962 when 75 chinook salmon were caught. Two of these fish bore fin clips that identified them as progeny of fall chinook salmon from the Snake River that had entered the reservoir in the spring. One fish of this group was also recaptured at the upper end of the main reservoir in the spring of 1963.

In early summer of 1963, fall chinook salmon were captured in gill nets in the lower Powder River Arm. As the environment improved in the fall, many fish moved into the upper arm. From mid-September to mid-December, 561 chinook salmon were captured; of these 444 were tagged and released. The subsequent capture of 28 marked fish in the area of release provided evidence that some fall chinook salmon remained in the upper arm until drawndown in December. On the basis of captures of tagged and untagged fish in the Powder River Arm, a population estimate (made by the technique of Schnabel, 1938) of chinook salmon in the arm ranged from 2,631 to 6,521; the average of 22 estimates was 3,883.

The movement of holdovers from Brownlee Reservoir in 1963 began in January and peaked in February. A total of 5,396 fish were caught in the skimmer net and in scoop traps below the dam. The exodus in 1964 started in November, peaked in January, and was completed by mid-May (Sims, 1970). The total catch of the skimmer net (partially deactivated in February) and the scoop traps was 1,275 fish. This early outmigration appeared to be a displacement because of the approach of a cold water mass through the reservoir (fig. 14).

The recapture of marked holdover fall chinook salmon within the reservoir in 1963 provided information on movements of these fingerlings. Early in the year (before April) most of the fish moved toward the dam, but many moved upstream and a few were recaptured in the area of release. The recapture of fish in all areas of the reservoir and the relatively slow rates of movement indi-

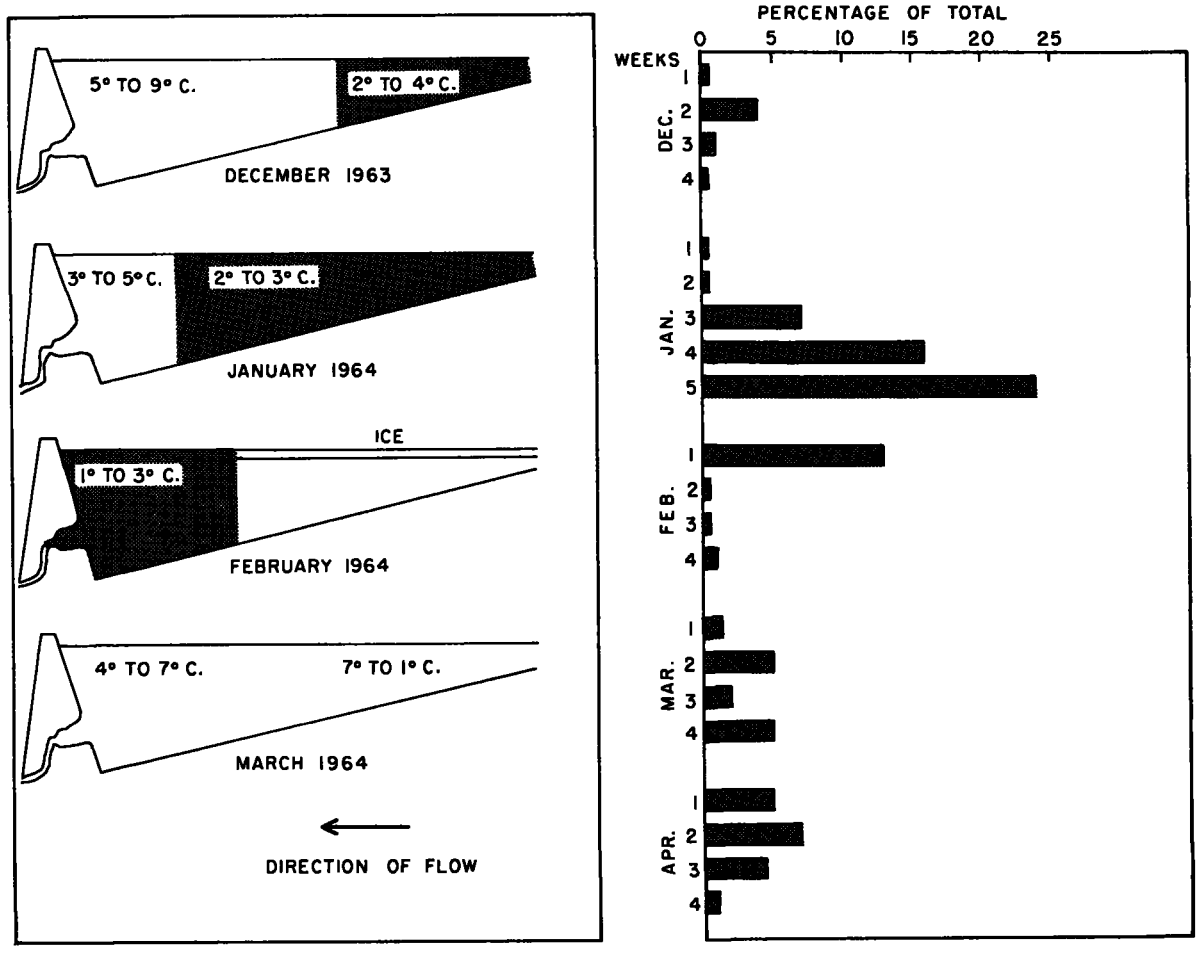

FIGURE 14.—Movement of holdover fall chinook salmon from Brownlee Reservoir in relation to water temperature. (The early outmigration coincided with the approach of a mass of cold water.)

cated that these fish were wandering. As the season progressed, however, the increases in the proportion and rate of movement downreservoir suggest the onset of a directed migration (fig. 15).

The holdover of fingerling salmon in Brownlee Reservoir was evident during each year of study, but the percentage of the total involved, as indicated from reservoir recruitment and escapement estimates (Krcma and Raleigh, 1970; Sims, 1970), fluctuated significantly. The percentage of holdovers seemed to be smallest in 1965, intermediate in 1964, and highest in 1963. The yearly percentage of holdovers varied inversely with reservoir conditions conducive to good passage of fish (figs. 4 and 5).

KOKANEE OF AGE-GROUP I

A few kokanee were caught in the reservoir in 1963 and 1964, and large numbers entered the reservoir in 1965 (table 3). The fish were probably from the Payette River system (Payette Lakes and Cascade and Deadwood Reservoirs). The migration appeared each year in early June, peaked in mid- to late June, and continued into July. Too few fish were present in 1963 or 1964 to determine movement within the reservoir. In 1965, however, it was evident from gill net catches and the recapture of tagged fish that through June the migrants consistently moved downreservoir. By mid-July, when the reservoir was full and the outflow was greatly diminished, fish were moving upreservoir and downreservoir in about equal numbers.

Kokanee were captured near the surface early in the migration, but as the season progressed and the environment deteriorated, the population was concentrated near the dam at depths of 18 to 47 m., as were other salmon species that held over (fig. 13).

TABLE 3.—*Estimated length and numbers of kokanee that entered Brownlee Reservoir, 1963–65 (from Krcma and Raleigh, 1970)*

Year	Fish	Length	
		Mean	Range
	Number	*Mm.*	*Mm.*
1963	500		
1964	5,500	120	104–146
1965	506,800	108	70–155

Kokanee populations that passed through Brownlee Reservoir did not do well. The fish that we observed did not leave their nursery area until late spring. They arrived at Brownlee Reservoir when the impoundment was filling or full, the temperatures were rising, and spillway flow was reduced. If they did not move through the reservoir, the harsh environment in late summer probably caused almost total mortality. Emigration estimates made by Sims (1970) suggested that losses were large in 1964 and 1965. These fish apparently were unable to survive through the summer—a few holdovers of the 1962 migration were captured in 1963, but none were observed in later years.

DISTRIBUTION AND MOVEMENT OF HATCHERY-REARED SALMON

To bolster the dwindling numbers of native salmon and to observe the effect of the reservoir on the passage of other salmon species, we placed hatchery-reared fall chinook and coho salmon juveniles in the Snake River about 120 km. above the reservoir in 1964 and introduced hatchery-reared sockeye and fall-chinook juvenile salmon about 88 km. above the reservoir in 1965 (Krcma and Raleigh, 1970).

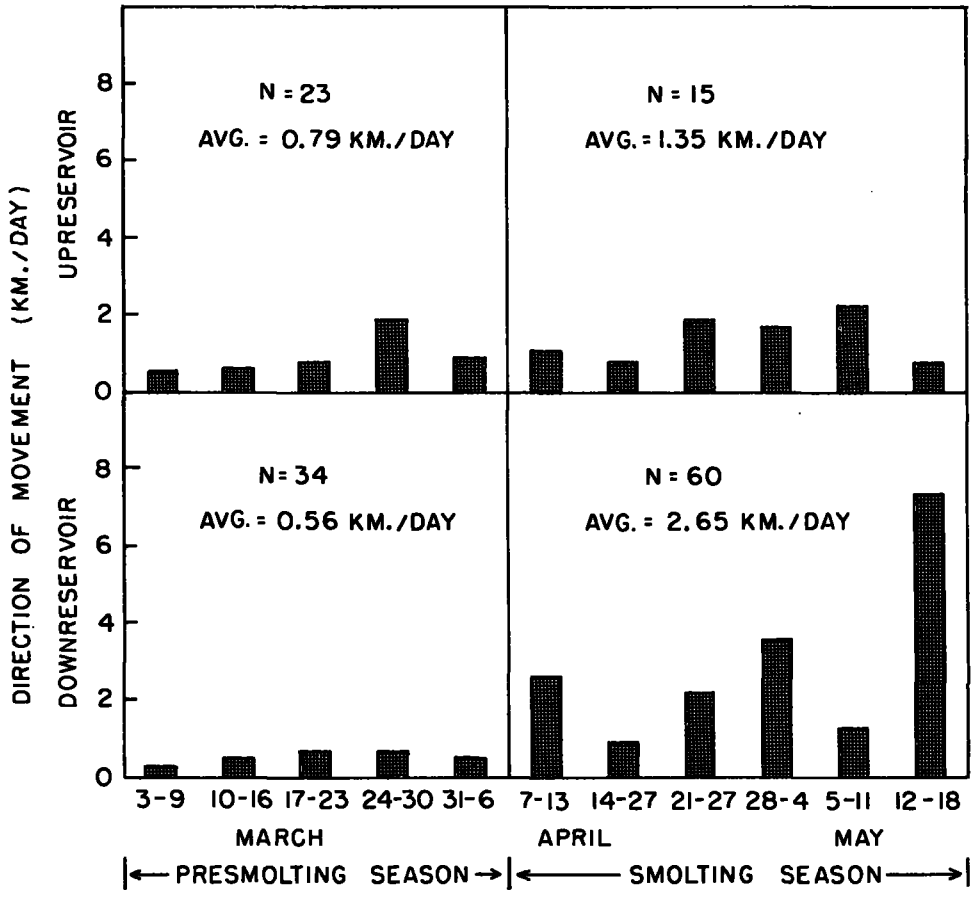

FIGURE 15.—Numbers of tagged juvenile chinook salmon holdovers recovered in Brownlee Reservoir, March 3 to May 18, 1963, showing direction and rate of movement.

FALL CHINOOK SALMON OF AGE-GROUP 0

Hatchery-reared fall chinook salmon were released in the Snake River about 120 km. above Brownlee Reservoir in March 1964 and 1965. Although released over a period of only 10 days, their movement into the reservoir extended over 3 months. Early and late migrants were 46 mm. and 130 mm. long in 1964 and 67 mm. and 135 mm. in 1965.

In 1964 and 1965, tagged hatchery chinook salmon moved primarily toward the dam until mid-May. After mid-May in 1964, some tagged fish were recaptured moving upreservoir; four tagged fish were recaptured in traps in the Snake River about 4 km. upstream from the head of the reservoir (Krcma and Raleigh, 1970). This upstream movement involved fewer fish in 1965. According to Sims (1970), 50 percent of the estimated migration of hatchery-reared chinook salmon into Brownlee Reservoir had left by the end of June 1964 and over 97 percent in 1965.

The movement upstream into the Snake River in 1964 might have been related to temperature, as noted previously for populations of native juvenile chinook salmon.

The ability of these fish to move through the reservoir to the river below Brownlee Dam (50 percent in 1964 and 97 percent in 1965) appeared to vary with volume of flow, direction of current, and length of reservoir. The drawdown lasted 6 weeks longer in 1965 than in 1964 and was accompanied by spillway discharges of large volume and duration and high volumes of inflow from the Snake River (fig. 4). During the 1965 migration this condition produced not only a smaller impoundment (45–50 km. long) but currents of higher velocity that were more consistently toward the dam than in 1964.

The rate of movement of tagged chinook salmon in the reservoir was similar in 1964 and 1965 even though the environments were different. The rate for all chinook salmon that moved toward the outlet averaged 3.0 and 2.9 km./day, respectively (table 4). Fish tagged through the first half of May generally moved faster than those tagged later. Upreservoir movement for nine chinook salmon averaged 0.89 km./day in 1964 and 2.0 km./day in 1965.

Chinook salmon recaptured downriver at Ice Harbor Dam averaged 19.9 km./day in 1964 and 18.8 km./day in 1965 through the reservoir and river.

Fish captured early in the season in midreservoir and along both banks indicated that fall chinook salmon of age-group O were distributed throughout the surface area. Gill net catches showed that juvenile chinook salmon moved both up and down the reservoir during darkness. This observation implies that most directed movement may have occurred during daylight and that fish milled or were carried by currents during darkness.

The distribution of hatchery-reared fall chinook salmon through the summer was similar to that of native fall chinook salmon (fig. 16). In the spring the fish were generally distributed throughout the epilimnion of the reservoir. As the surface temperature increased the fish moved into deeper water and downreservoir. Temperatures above 21° C. at the surface and low oxygen concentrations (less than 3 p.p.m.) at depths where the water was cooler forced the fish to move into restricted areas. The increased catches of fish in gill nets in the upper reservoir in June and July were probably the result of fish returning from a temporary upstream movement into the Snake River.

Some hatchery-reared chinook salmon from the 1964 release remained in Brownlee Reservoir during the winter. Sims (1970) estimated that only about 85 percent of the hatchery-reared fall chinook salmon that entered the reservoir in 1964 migrated out that year. Also 17 fish from this group were captured in the reservoir in February and March 1965.

TABLE 4.—*Summary of direction and rate of movement of tagged age-group O hatchery-reared fall chinook salmon in Brownlee Reservoir, 1964–65*

Year	Direction of movement				Rate of movement					
	Recaptured	Upreservoir	Downreservoir	No movement	Upreservoir	Range	Downreservoir	Range	Brownlee Reservoir to Ice Harbor	Range
	Number	*Number*	*Number*	*Number*	*Km./day*		*Km./day*		*Km./day*	
1964	60	9	37	14	0.89	0.06–1.85	3.0	0.31–9.7	19.9	12.6–33.8
1965	277	14	237	46	2.0	.08–9.76	2.9	.06–8.7	18.8	8.0–42.0

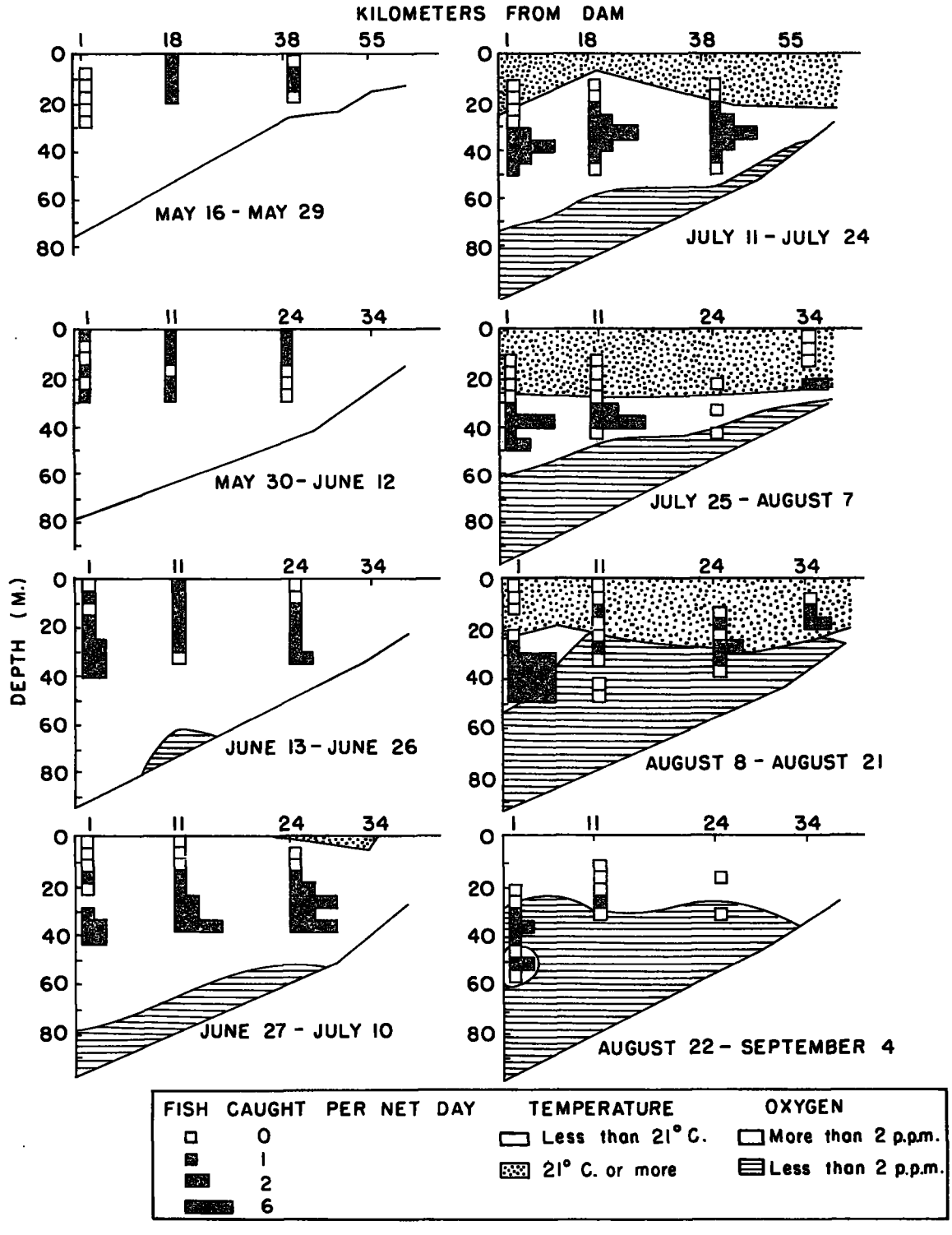

FIGURE 16.—Distribution of hatchery-reared fall chinook salmon in Brownlee Reservoir in relation to critical oxygen and temperature regimes as determined from gill net catches, 1965.

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COHO SALMON OF AGE-GROUP I

Of 375,000 juvenile coho salmon released in the Snake River 120 km. above the reservoir from March 15 to 30, 1964, an estimated 69,000 entered the reservoir (Krcma and Raleigh, 1970). Early in the migration these fish averaged 112 mm. long; by the end they averaged 131 mm.

On the basis of peak catches at the Snake River trapping site above the reservoir and at the dam, passage time through the reservoir was 2 weeks (fig. 17). The reservoir was only 64 km. long at the beginning of the migration as a result of a 13.5-m. drawdown; the distance between the reservoir and the trapping site in the river was about 35 km.

Recapture data from 26 tagged fish indicated that the rate of movement changed during the migration (fig. 18). Before May 20 when the reservoir was drawn down about 13 m. and the outflow volume was large (about 850 c.m.s.), 17 tagged migrants averaged 1.8 km./day. As the outflow was curtailed and the reservoir began to fill, the migration rate of nine tagged fish then dropped to 0.9 km./day. At this time the proportion of fish moving upreservoir also appeared to increase.

In early May most coho salmon were near the surface in the upper reservoir, but by the end of the month most had shifted to the vicinity of the dam at greater depths. As the migration rate slowed in late May and recruitment from the Snake River continued, catches were again good in the upper reservoir. In July the greatest concentration appeared to be in midreservoir at depths of 18 to 31 m. Catches declined through July, and only a few fish were captured thereafter.

SOCKEYE SALMON OF AGE-GROUP I

In 1965, 473,000 yearling sockeye salmon were released in the Snake River, 88 km. above Brownlee Reservoir. Krcma and Raleigh (1970) estimated that 360,000 had entered the reservoir. The salmon were from Babine Lake, British Columbia and reared to yearling stage at the Leavenworth National Hatchery, Wash. The left ventral fin was clipped on all fish. Migrants in March averaged 121 mm.; later migrants averaged 130 mm. by mid-May.

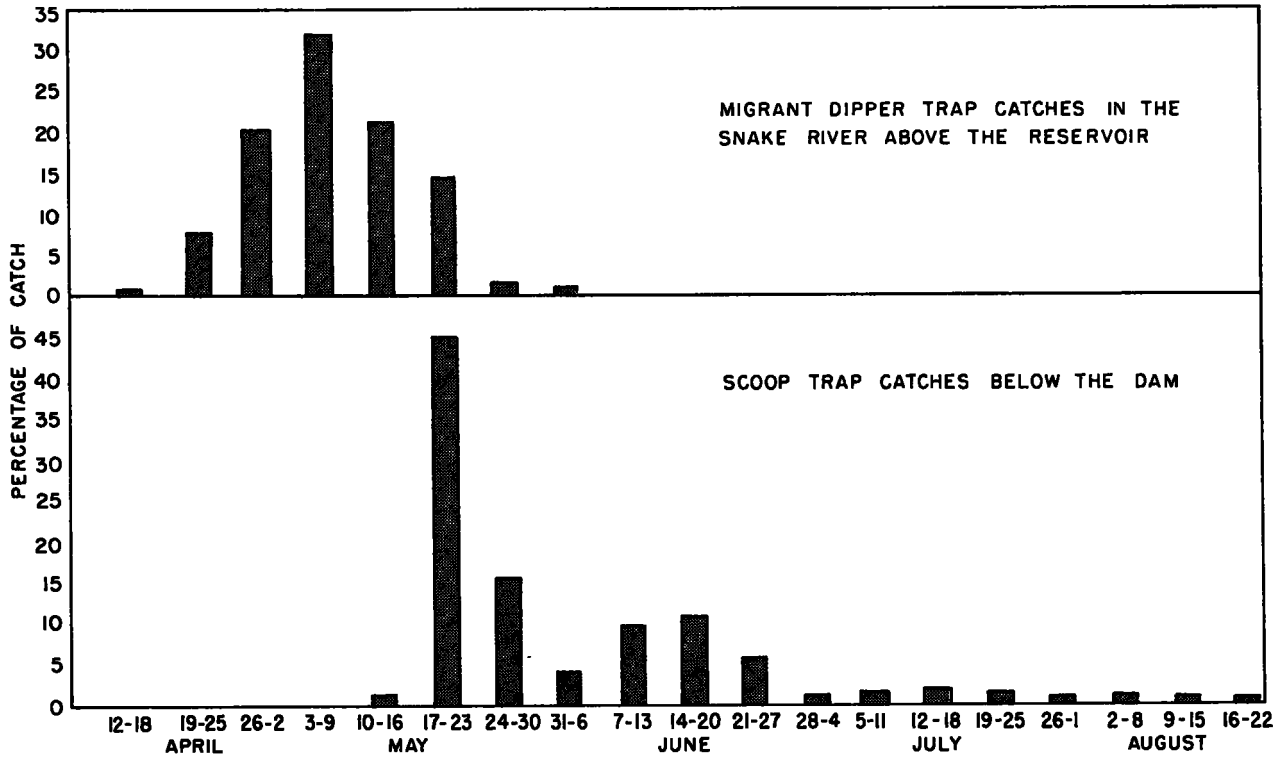

FIGURE 17.—Weekly catches of juvenile hatchery-reared coho salmon above Brownlee Reservoir and below Brownlee Dam, 1964.

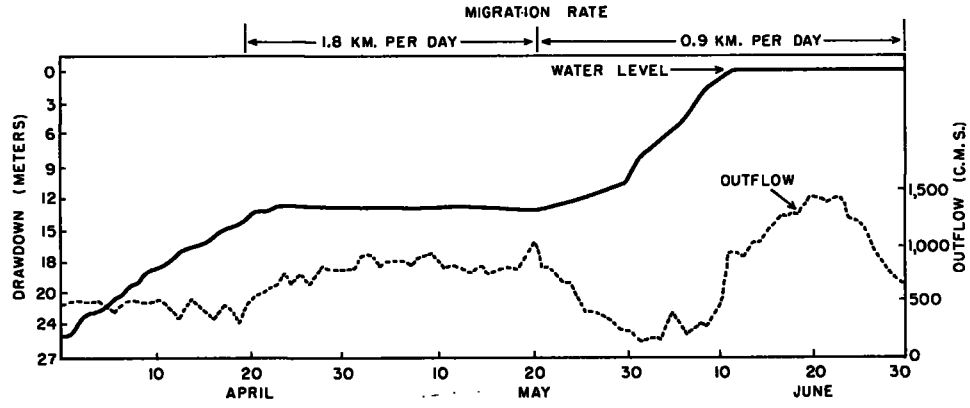

FIGURE 18.—Rate of downstream movement of tagged hatchery-reared coho salmon in relation to water level and outflow in Brownlee Reservoir, April 1 to June 30, 1964.

These fish moved rapidly downstream after release. The first sockeye salmon were captured in the reservoir on March 17—2 days after the initial release. Catches above the reservoir reached a peak during the first week of April and below the reservoir the following week. During the ensuing 2 months, 44 sockeye salmon were recaptured at Ice Harbor Dam and two at Bonneville Dam. The capture of fish in gill nets in the reservoir indicated that the fish moved consistently downreservoir. No sockeye salmon were observed in the Powder River Arm, and no delay within the reservoir was evident.

The average daily rate of movement for 117 tagged sockeye salmon that moved toward the outlet was 5.2 km./day. On the basis of this rate and the length of the reservoir (45–50 km.) in late March and early April, sockeye salmon required an average of about 8 or 9 days to move through the reservoir.

Most sockeye salmon were captured within 4.5 m. of the surface, some were between 4.5 and 13.5 m., and a few were taken as deep as 22.5 m. (table 5). Data on catch per unit of effort at three gill net stations indicated that the vertical distribution was similar throughout the reservoir.

Sockeye salmon were captured near shore and offshore in the upper reservoir. In the lower reservoir they were captured almost exclusively offshore. The recovery of tagged sockeye salmon indicated that fish tagged near the shore eventually moved to the open water, whereas those tagged offshore remained offshore.

During the migration period from March through mid-May 1965, the environment was favorable for fish passage. Dissolved oxygen concentrations were 6 to 11 p.p.m. until early May, and temperatures ranged from about 5° C. in late March to 15° C. in late April. The reservoir level was 24 to 30 m. below full pool through mid-May, and its length was reduced to about 45 km. Spill discharge at Brownlee Dam was continuous, ranging from a weekly average of 424.5 to 1,440.3 c.m.s. Current monitors, operated by personnel studying the limnology of the reservoir, revealed that surface currents were oriented toward the outlet. Ac-

TABLE 5.—*Depth distribution of sockeye salmon yearlings as indicated by the catch per gill net day at different depths in Brownlee Reservoir, March 17 to April 26, 1965* [1]

Depth	Mile 1			Mile 12			Mile 24		
	Sets	Sockeye	Catch per unit effort	Sets	Sockeye	Catch per unit effort	Sets	Sockeye	Catch per unit effort
M	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
<1.4	7	247	35.3	4	312	78.0	6	205	34.2
1.5– 4.1	2	3	1.5	3	8	2.7	3	10	3.3
4.2–13.7	5	4	0.8	4	3	0.8	6	10	1.7
13.8–18.3	2	0	0.0	3	3	1.0	4	3	0.8
18.4–22.9	5	3	0.6	1	4	4.0	4	3	0.8
23.0–27.5	2	0	0.0						

[1] Mesh sizes used were 1.9, 2.5, 3.1, and 3.8 cm. stretched mesh.

cording to Sims (1970), nearly 100 percent of the sockeye salmon migration had passed through Brownlee Reservoir.

SUMMARY

The distribution and movement of juvenile salmon that migrate through Brownlee Reservoir, a large impoundment on the Snake River, was studied from 1962 to 1965. The study included native spring and fall chinook salmon and kokanee and hatchery-reared fall chinook, coho, and sockeye salmon.

Each native salmon population had a characteristic age, size, and time of entry into the reservoir. Most spring chinook salmon from Eagle Creek entered the reservoir in the late fall as age-group O, 53 to 125 mm. long. These fish overwintered in the reservoir, primarily in the Powder River Arm. They resumed their seaward migration in the spring just before the peak of a second outmigration from Eagle Creek in March and April of age-group I fish, 65 to 138 mm. long. The migration of juvenile spring chinook salmon from the Weiser River entered the reservoir in peak numbers in late April or early May; it consisted of age-group I fish, 106 to 176 mm. long. This movement was closely followed by that of age-group O fall chinook salmon from the Snake River, 33 to 105 mm. long, which entered the reservoir in peak numbers in mid-May. Kokanee migrants entered the reservoir latest in the season; age-group I fish, 70 to 155 mm. long, arrived in mid-June.

Hatchery-reared groups of salmon migrated into the reservoir as follows: fall chinook salmon of age-group O (46–135 mm.) in mid-May of 1964 and 1965; coho salmon of age-group I (71–166 mm.) in mid-May 1964; and sockeye salmon of age-group I (86–175 mm.) in early April 1965.

Migrants from all populations were near the surface as they entered. As the season progressed and the juvenile fish moved downreservoir, they tended to move into deeper water.

Migration peaks from the reservoir varied from year to year, depending on reservoir conditions, but were sequential by stock. Fish (mainly fall chinook salmon) that remained in the reservoir from the previous year's migration left the reservoir early (late January or February) at the approach of a cold water mass that moved through the reservoir. This migration was followed in late February and early March by fish (mainly fall chinook salmon) that had overwintered in the Powder River Arm. Spring migrants from Eagle Creek and Weiser River arrived at the dam in large numbers in April and May. Fall chinook salmon from the Snake River arrived in late May to early July and kokanee, in July or August. Hatchery-reared fall chinook salmon left in May 1964 and in April 1965, coho salmon in late May 1964, and sockeye salmon in April 1965.

Juvenile fish that did not leave the reservoir by late June or July were confined to restricted areas of the reservoir by high epilimnion temperatures and low concentrations of dissolved oxygen, which extended into the epilimnion from the hypolimnion. When this process began, juvenile salmon in the upper end of the reservoir usually reentered the slightly cooler waters of the Snake River. They returned to the reservoir when temperatures in the river began to approach 20° C. The survival of holdover salmon through the summer and early fall was extremely poor.

The differences in success of passage through the reservoir were more closely related to the physical conditions of the reservoir than to behavioral differences between species of salmon stocks. Success of passage for all populations was poorest in 1963 when the reservoir was nearly full throughout the migration. Under this condition, the reservoir was 92 km. long and surface currents were either weak or nonexistent and often moved upreservoir. Passage through the reservoir was intermediate in 1962 and 1964 when drawdown was 6 to 14 m. through May and the reservoir averaged 70 km. long. The most successful passage was in 1965 when the drawdown was large (26–28 m. through May), the reservoir was relatively small (45–50 km. long), and currents were consistently oriented downstream. Loss of orientation and upreservoir movement of the juvenile salmon were correlated with conditions in the reservoir most prevalent in 1963 and least prevalent in 1965.

Early entrance into the reservoir appeared to improve the chances of successful passage. In general, early fish encountered the best combination of reservoir length, current conditions, and environment. Late migrants, such as the kokanee, entered a rapidly deteriorating environment, and their success of passage was extremely poor.

ACKNOWLEDGMENTS

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EMIGRATION OF JUVENILE SALMON AND TROUT FROM BROWNLEE RESERVOIR, 1963–65

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ABSTRACT

Floating scoop traps below Brownlee Dam captured samples of marked and unmarked salmon and trout that had left the impoundment from July 1963 through August 1965; estimates of emigration were based on these samples.

Success of passage varied among years and populations and was affected by the environment in the reservoir during outmigration. Downstream migrants that entered the reservoir early in the season were more successful than those that entered later. Emigration was also more successful when the reservoir level was low.

Brownlee Reservoir was chosen for an extensive research program by BCF (Bureau of Commercial Fisheries) to determine how a large impoundment affects the passage of salmon and trout. The research, begun in the spring of 1962, consisted of five studies: (1) limnology of the reservoir system (Ebel and Koski, 1968); (2) upstream migration of adult chinook salmon (*Oncorhynchus tshawytscha*) through the reservoir (Trefethen and Sutherland, 1968); (3) migration of juvenile salmon and trout into the reservoir (Krcma and Raleigh, 1970); (4) distribution and movement of juvenile salmon in the reservoir (Durkin, Park, and Raleigh, 1970); and (5) migration of juvenile salmon and trout from the reservoir (the present report).

Brownlee Reservoir, on the middle Snake River, lies at the southern end of Hells Canyon along the border between northeast Oregon and western Idaho. The reservoir is about 92 km. long and averages slightly less than 800 m. wide. Brownlee Dam (constructed by the Idaho Power Company) is a high-head structure, the primary function of which is hydroelectric power production. It is 396 m. wide on the top, has a single spillway and four Francis turbines with vertical shafts, and creates 83 m. of head at full pool. The dam discharges directly into Oxbow Reservoir, formed by Oxbow Dam about 19 km. downstream.

In an attempt to provide facilities for the passage of juvenile salmon and trout past Brownlee Dam, the Idaho Power Company installed a fingerling-collection system in 1959 in the forebay of the reservoir about 3 km. downstream from the dam (Soule, Heikes, Mitchell, and Schaufelberger, 1959). The system, consisting of a shore-to-shore barrier net and surface collection traps, proved only partly successful.[1] Many fingerlings passed under or through the barrier net and left the reservoir via the turbines or spillway. Idaho Power Company removed the system in February 1964, after which all fish that left the reservoir passed through the turbines or spillway.

Native populations of anadromous salmon and trout affected by Brownlee Reservoir include fall- and spring-run chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Salmo gairdneri*). Before the construction of Brownlee Dam in 1958, the largest population was fall-run chinook salmon, which spawned in the Snake River upstream from what is now the upper end of Brownlee Reservoir. The Fish Commission of Oregon estimated annual fall chinook salmon spawning runs of as many as 20,000 fish in the late 1950's. By 1963 this population was greatly reduced. Before 1963, spring-run chinook salmon spawned in the Weiser River (a tributary of the Snake River above the head of the reservoir) and in Eagle Creek (a tributary of the Powder River, which enters near the lower end of the reservoir). Steelhead trout were native to Weiser River and Eagle Creek as well as several

[1] Graben, James E. 1964. Evaluation of fish facilities, Brownlee and Oxbow Dams, Snake River. Idaho Department of Fish and Game, Boise, Idaho, 60 pp. (Processed.)

Published April 1970.

streams above Brownlee Dam. Several impoundments in the Snake River system above Brownlee Reservoir support populations of kokanee (*O. nerka*); these fish periodically move into the Brownlee area.

After the decline of the native runs, hatchery-reared chinook, coho (*O. kisutch*), and sockeye salmon were released in the Snake River above Brownlee Reservoir by the BCF in 1964 and 1965 to provide additional fish for study.

The study on the passage of juvenile salmon and trout from Brownlee Reservoir began in July 1963 and continued through the summer of 1965. I report here the number and size of emigrants and the time of emigration.

TECHNIQUES OF SAMPLING AND ANALYSIS

The sampling area (fig. 1) was immediately below Brownlee Dam. About 180 m. below the powerhouse the turbine tailrace channel enters the original river channel, which carries the intermittent discharges from the spillway of the dam. The Interstate Bridge crosses Oxbow Reservoir about 600 m. downstream from the dam. At that point, the reservoir is about 160 m. wide and 3.5 m. deep at midchannel when Oxbow Reservoir is at full pool.

The primary sampling site was in the turbine tailrace, about 150 m. below the powerhouse. The turbine tailrace is about 76 m. wide; the water is about 4 m. to 7 m. deep, depending on the level of Oxbow Reservoir and the discharge from Brownlee Dam. Because fish that passed over the spillway could not be sampled at the tailrace site, an additional sampling site was established downstream at the Interstate Bridge for use during periods of spillway operation.

The analyses of the data involved an evaluation of (1) equipment, (2) procedures, (3) tests of sampling efficiency, and (4) methods of computing emigration.

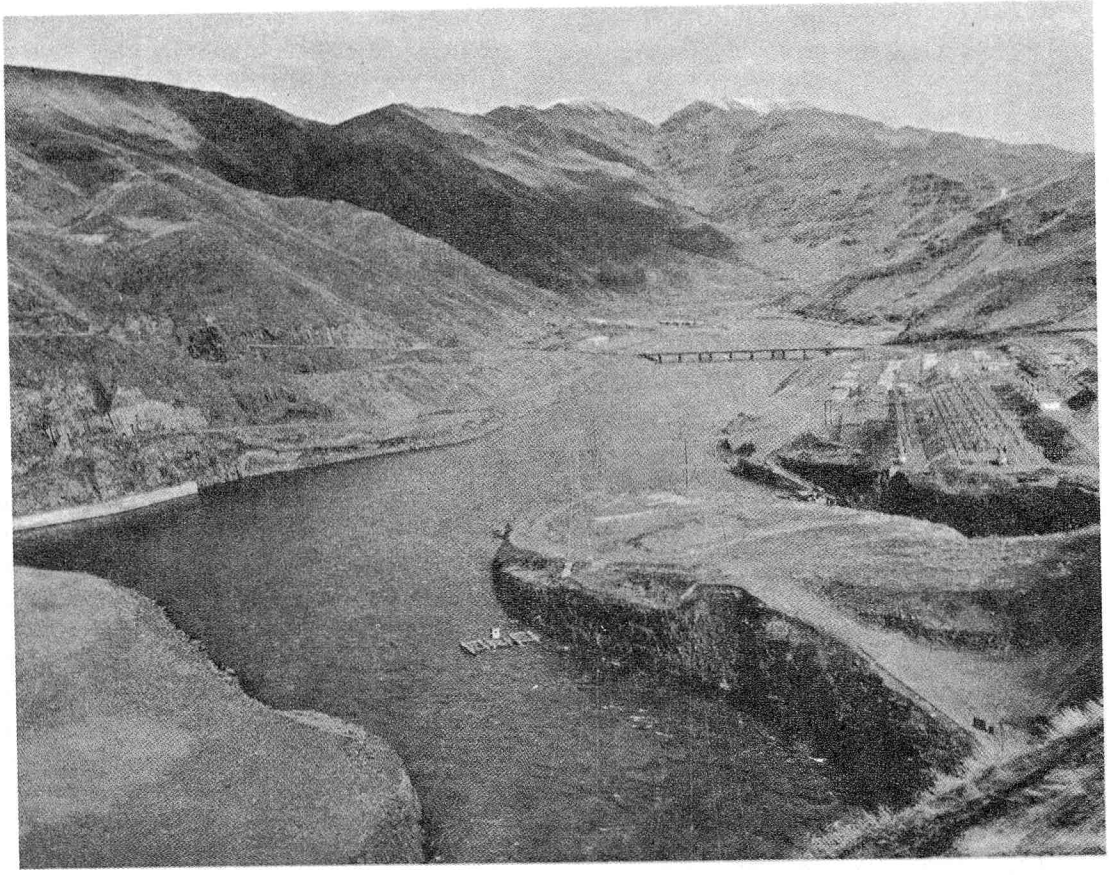

FIGURE 1.—Turbine tailrace (foreground) at Brownlee Dam with scoop traps in position below right bank. Spillway (not in operation in this photo) enters original river channel on extreme left.

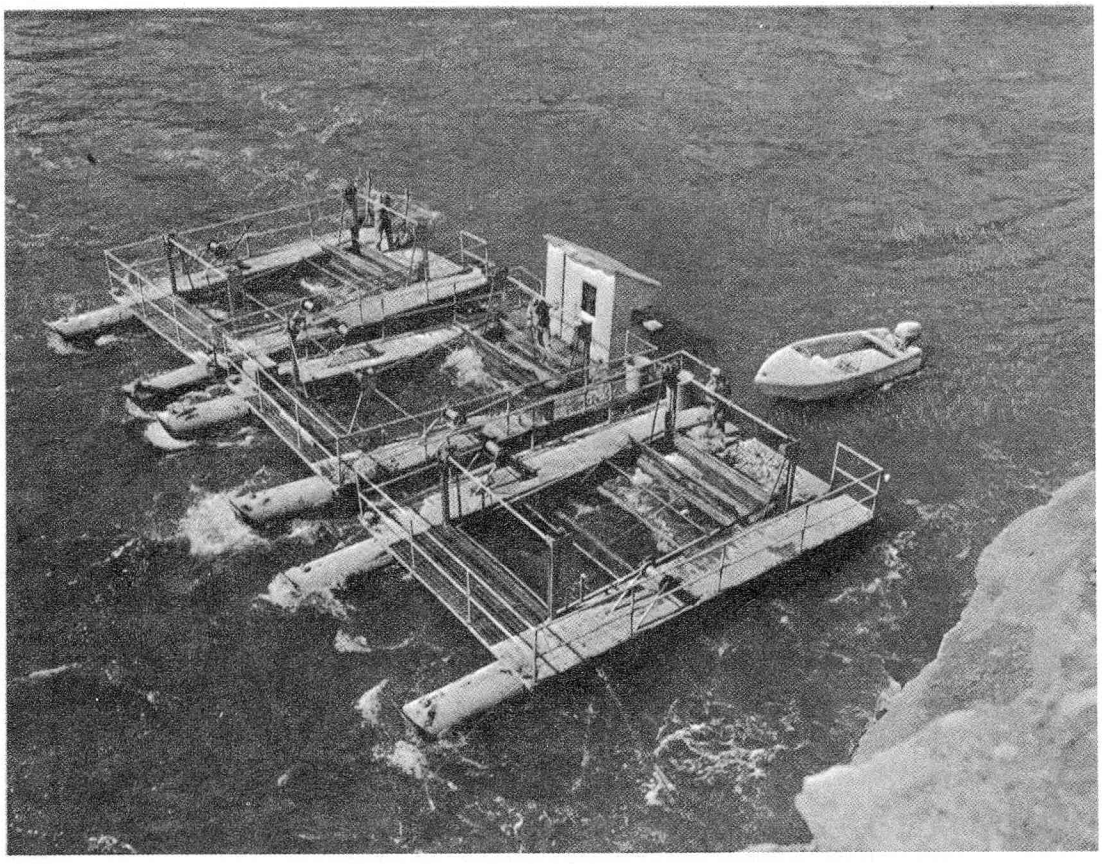

FIGURE 2.—Scoop traps in operation in the turbine tailrace.

EQUIPMENT

Three scoop traps (fig. 2) were used to collect juvenile migrants.[2] Each trap was 3.0 m. wide by 3.2 m. long and fished at a depth of 1.2 m. A pontoon-type barge, 5.5 m. by 7.5 m., supported the individual traps and winch equipment. In the turbine tailrace, the traps were close to the right (Idaho) bank. At the Interstate Bridge, one trap was in the center of the channel and the other two were about 30 m. from the right and left banks.

PROCEDURES

The traps were emptied of fish and cleared of debris at 8 a.m. and 4 p.m. Additional checks were made at noon and at midnight during peak outmigration and at any time that excessive debris accumulated. During special studies, the traps were emptied of fish and debris at intervals of 1, 4, and 6 hours.

All salmon and trout were identified, examined for marks or tags, and measured for fork and standard length. All live salmon and trout were anesthetized before examination and then were released unless needed for special studies. Scale samples were taken from dead and injured fish when possible.

TESTS OF TRAP EFFICIENCIES

Fish marked by partial fin clip, tattoo, or thermal brand were used to evaluate the efficiency of the scoop traps at both sampling sites. Hatchery-reared juveniles were used for marking in all years, except in 1964 when a few tests were made with native age-group I spring and fall chinook salmon from scoop trap catches. Hatchery-reared age-group 0 chinook salmon were used in 1964 and 1965, age-group I coho salmon in 1964, and sockeye salmon in 1965.

Tests at the Interstate Bridge required that test fish be released into the spillway and into the turbine penstocks; tests at the turbine tailrace site required releases only into the penstocks. Pen-

[2] Bell, Robert. 1959. Time, size, and estimated numbers of seaward migrations of chinook salmon and steelhead trout in the Brownlee-Oxbow section of the middle Snake River. Idaho Department of Fish and Game, Boise, Idaho, 34 pp. (Processed.)

stock releases were made by pumping the test fish down the penstock air vent through a 76-mm. hose.

In 1964, about 1,570 hatchery-reared juvenile chinook salmon and an equal number of juvenile coho salmon were released into the spillway and turbine penstocks to determine efficiency of the traps at the Interstate Bridge (table 1). Fifteen chinook and 15 coho salmon were recaptured, (0.95-percent return for each species). Trapping efficiency for chinook salmon was slightly higher in 1965 when 1,171 hatchery-reared test fish were released and 15 fish (1.28 percent) were recaptured (table 2). Recovery efficiency of the traps for hatchery-reared sockeye salmon fingerlings released in 1965 was significantly higher than for chinook salmon; 2,670 test sockeye salmon were released and 71 (2.66 percent) were recaptured at the bridge site (table 3).

The scoop traps were more efficient in the turbine tailrace than at the Interstate Bridge. In 1964–65, 8,471 test fish (hatchery-reared juvenile chinook, coho, and sockeye salmon) were released into the various turbine penstocks for recovery in the turbine tailrace. Differences in average recovery between years and among species were so slight that the data were combined. Recoveries for daylight releases (8:00 a.m. to 4:00 p.m.) were 0.5 to 7.5 percent and averaged 4.1 percent (table 4). Recaptures of fish from night releases (4:00 p.m. through 8:00 a.m.) were 4.5 to 29.7 percent and averaged 11.3 percent (table 5).

METHODS OF COMPUTING EMIGRATION

Estimates of emigration were based on live and dead fish caught in the scoop traps. Identity of the various populations was determined from fish that had been marked in the tributary drainages and subsequently recovered in the scoop traps. Length-frequency data and scale samples were also used to determine the origin of different populations of fish emigrating at various times of the year.

Estimates of emigration during periods of sampling at the Interstate Bridge were computed with the general formula (Chapman, 1948):

$$N_1=\frac{C(M+1)}{(R+1)} \qquad (1)$$

where

N=population estimate
C=sample size
M=number of marks
R=marked recaptures in C

TABLE 1.—*Numbers of marked juvenile chinook and coho salmon recovered in scoop traps at the Interstate Bridge after release in the spillway (S) or turbines (T) of Brownlee Dam, April 24 to June 30, 1964*

Date (1964)	Fish released	Release site	Average spill	Fish recovered	
	Number		(*M.³/sec.*)	*Number*	*Percent*
April:					
24	101	S	177	1	0.99
25	100	S	185	1	1.00
26	103	S	279	1	.97
27	95	S	405	0	.00
28	100	S	458	0	.00
29	100	S	452	1	1.00
May:					
7	106	S	548	4	3.77
7	89	T	548	4	4.49
8	100	S	642	0	.00
8	100	T	642	1	1.00
15	100	T	510	0	.00
16	100	T	510	2	2.00
20	102	S	579	1	.98
20	100	T	579	0	.00
21	116	T	551	2	1.72
27	106	T	0	1	.94
June:					
11	79	S	332	1	1.27
14	179	S	708	1	.56
15	189	S	737	2	1.06
16	200	S	795	2	1.00
16	200	T	795	1	.50
17	100	T	978	0	.00
18	100	T	1,100	1	1.00
19	100	T	1,136	1	1.00
23	100	S	1,189	0	.00
24	100	S	1,137	1	1.00
25	100	S	961	1	1.00
30	100	S	170	0	.00
Total	3,165			30	.95

TABLE 2.—*Numbers of marked juvenile chinook salmon recovered in scoop traps at the Interstate Bridge after release in the spillway (S) or turbines (T) of Brownlee Dam, April 9 to May 20, 1965*

Date (1965)	Fish released	Release site	Average spill	Fish recovered	
	Number		(*M.³/sec.*)	*Number*	*Percent*
April:					
9	160	S	409	1	0.6
13	102	T	566	2	2.0
13	121	S	566	0	.0
15	107	S	512	2	1.9
21	122	T	1,338	1	.8
25	154	T	1,557	2	1.3
May:					
14	101	S	958	1	1.0
14	106	T	958	2	1.9
20	101	S	622	3	3.0
20	97	T	622	1	1.0
Total	1,171			15	1.28

To compensate for the variation in efficiency of traps in the turbine tailrace, I computed emigration during periods of sampling at that site with an alternate method:

$$N_2=\frac{\text{trap catch}}{\text{percentage of efficiency}} \qquad (2)$$

Upper and lower limits were computed for estimates of emigration at both sampling sites. For estimates based on sampling at the Interstate

TABLE 3.—*Numbers of marked juvenile sockeye salmon recovered in scoop traps at the Interstate Bridge after release in the spillway (S) or turbines (T) of Brownlee Dam, March 31 to May 15, 1965*

Date (1965)	Fish released	Release site	Average spill	Fish recovered	
	Number		*(M.³/sec.)*	*Number*	*Percent*
March:					
31	241	T	487	6	2.5
April:					
1	95	S	459	2	2.1
2	109	T	425	2	1.8
5	177	S	448	4	2.3
5	275	T	448	8	2.9
6	140	S	519	2	1.4
7	211	T	338	4	1.9
8	238	S	357	5	2.1
9	102	T	409	5	4.9
10	218	S	510	4	1.8
10	103	T	510	3	2.9
11	124	S	511	6	4.8
12	180	S	499	2	1.1
14	110	T	448	4	3.6
15	140	S	511	5	3.6
May:					
15	207	S	511	9	4.3
Total	2,670			71	2.66

TABLE 4.—*Numbers of marked juvenile salmon (chinook, coho, and sockeye) recovered in scoop traps in the Brownlee Dam tailrace between 8 a.m. and 4 p.m., 1964–65*

Date	Total fish released	Number released at turbine number				Turbine discharge	Fish recovered	
		1	2	3	4			
	Number	*Number of fish*				*(M.³/sec.)*	*Number*	*Percent*
1964:								
July 3	200	100			100	618	5	2.5
July 3	200	100			100	612	7	3.5
July 4	200	100			100	439	14	7.0
July 4	200	100			100	448	7	3.5
July 5	200	100			100	379	6	3.0
July 5	200	100			100	399	1	.5
July 5	200	100			100	375	3	1.5
July 7	200		100	100		387	15	7.5
July 7	200		100	100		443	10	5.0
July 7	200		100	100		417	10	5.0
July 8	200		100	100		536	9	4.5
1965:								
June 5	350	96	99	76	79	472	13	3.7
June 5	371	99	100	79	93	472	17	4.6
June 6	392	106	99	87	100	409	22	5.6
June 7	384	95	92	105	92	547	12	3.1
Total	3,697	1,096	790	747	1,064		151	4.11

Bridge, these limits represent the 95-percent confidence limits as computed by Chapman's formula:

$$\overline{m},\ \underline{m}=\mathrm{R}+\frac{1.96^2}{2}\pm 1.96\sqrt{\mathrm{R}+\frac{1.96^2}{4}} \qquad (3)$$

where

$\overline{m}$ and $\underline{m}$ are the upper and lower values of R, respectively.

Upper and lower estimates at the turbine tailrace site were based on the 95-percent confidence interval of the means of the frequency distributions in the respective day-night tests of efficiency (Wilkes, 1948). These values were computed according to the formula:

$$u=\overline{X}\pm t_a\frac{s}{n}$$

where

u=population mean
$\overline{X}$=sample mean
t_a=confidence coefficient
s=standard deviation
n=number of tests

TABLE 5.—*Numbers of marked juvenile salmon (chinook, coho, and sockeye) recovered in scoop traps in the Brownlee Dam tailrace between 4 p.m. and 8 a.m., 1964–65*

Date	Total fish released	Number released at turbine number				Turbine discharge	Fish recovered	
		1	2	3	4			
	Number	*Number of fish*				*(M.³/sec.)*	*Number*	*Percent*
1964:								
July 3	200	100			100	577	10	5.0
July 4	200	100			100	378	9	4.5
July 5	200	100			100	349	13	6.5
July 7	100			100		364	7	7.0
July 11	300	100	100	100		268	25	8.3
July 11	300	100		100	100	263	26	8.7
July 12	200	100		100		228	34	17.0
July 12	200		100	100		294	34	17.0
July 14	200	100		100		301	15	7.5
July 15	100	100				84	6	6.0
July 15	300	100		100	100	343	27	9.0
July 15	200			100	100	214	28	14.0
July 16	300		100	100	100	339	89	29.7
July 17	200	100		100		303	12	6.0
July 18	300		100	100	100	408	34	11.3
1965:								
June 5	409	110	100	99	100	553	36	8.8
June 5	364	61	99	99	105	168	54	14.8
June 6	381	94	96	101	90	159	52	13.6
June 7	320	98	98	59	65	358	30	9.4
Total	4,774	1,363	793	1,458	1,160		541	11.33

Estimates of annual emigration were based on scoop trap catches from May 1963 through August 1965 (table 6). No tests of efficiency of scoop traps were made in 1963; therefore, estimates of emigration for that year were based on efficiency tests in 1964. In the estimates of emigration, catches by the Idaho Power Company barrier net in 1964 were also included. Estimates of immigration used to compare with estimates of emigration were from Krcma and Raleigh (1970).

ESTIMATES OF EMIGRATION

EMIGRATION OF NATIVE SALMON

The migration of juvenile salmon and trout from Brownlee Reservoir included three native and three hatchery-reared salmon populations and a trout population of unknown origin. Estimates of emigration were made for each population.

Native juvenile salmon migrating through Brownlee Reservoir included fall chinook salmon and kokanee from the Snake River and spring chinook salmon from Eagle Creek and the Weiser River.

TABLE 6.—*Catches of juvenile salmon and rainbow-steelhead trout by scoop traps below Brownlee Dam, May 1, 1963 to August 31, 1965* [1]

Date (year and month)	Chinook salmon	Coho salmon	Sockeye salmon	Kokanee salmon	Rainbow-steelhead trout
1963:	*Number*	*Number*	*Number*	*Number*	*Number*
May	2				
June	194				
July	62				
August	82				13
September	16				1
October	8				1
November	49				1
December	101				
1964:					
January	247				14
February	273				11
March	370				28
April	385				114
May	505	256			79
June	621	262		2	76
July	56	124		11	51
August	114	84		90	32
September	25	3		2	3
October	7			1	4
November	8				4
December	2				3
1965:					
January	2				2
February	2				
March	14		2,214		9
April	2,198		8,162		338
May	900		8		392
June	1,802			80	142
July	111			193	34
August	208			3,077	128
Total	8,864	729	10,384	3,456	1,480

[1] Catches by scoop trap reported by Graben, 1964 (see text footnote 1).

Fall Chinook Salmon

An estimated 54,800 native fall chinook salmon from the Snake River left the reservoir in 1963 as age-group 0 and in 1964 as age-group I (table 7). Of these fish, 2,700 were captured by the Idaho Power Company barrier net in the forebay of the reservoir and transported below Oxbow Dam and released. Total emigration of the 1963 year class was about 15 percent of established immigration to the reservoir (table 7).

Age-group-0 fish from the 1963 year class first appeared in the scoop traps below the dam in May 1963 (fig. 3); peak migration was in June. Except for one period in 1963 (late September to early October), some fish moved past the dam throughout the summer and fall. About 75 percent of age-group I fish in 1964 (1963 year class) left the reservoir in late January; a second peak appeared in early April.

Spring Chinook Salmon

Emigration of juvenile spring chinook salmon of the 1963 year class was 5,900 fish or about 16 percent of the estimated immigration from the Weiser River and Eagle Creek to the reservoir (table 8). A small number from Eagle Creek began

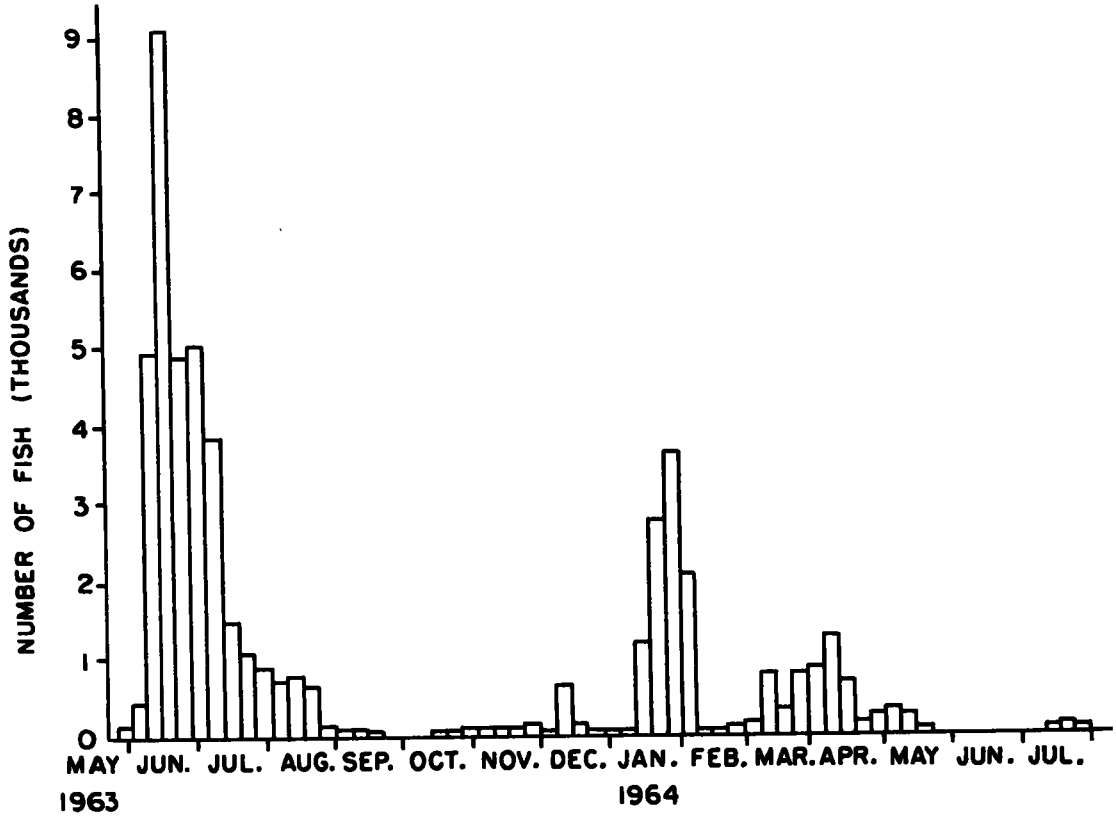

FIGURE 3.—Estimated emigration from Brownlee Reservoir of juvenile native fall chinook salmon (1963 year class), from the Snake River, May 1963 to August 1964.

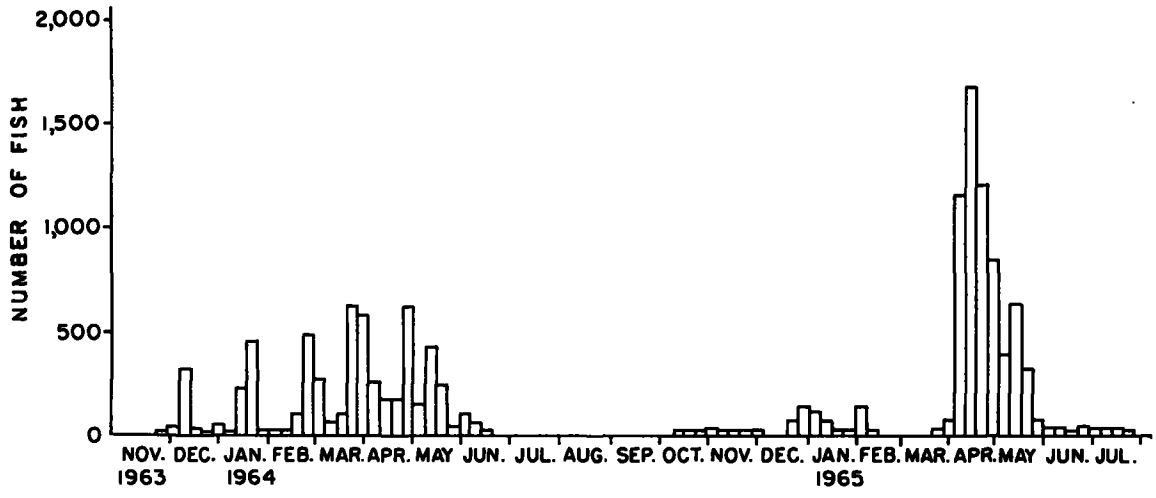

FIGURE 4.—Estimated emigration from Brownlee Reservoir of juvenile native spring chinook salmon from Eagle Creek and Weiser River, November 1963 to July 1965.

TABLE 7.—*Estimated immigration of juvenile native fall chinook salmon into Brownlee Reservoir from the Snake River and estimated emigration from the Reservoir, May 1, 1963 to August 1964 (all fish of 1963 year class)*

Estimated immigration	Years of emigration	Estimated emigration		Range of estimated emigration	
				Low	High
Number		*Number*	*Percent*	*Number*	*Number*
374,000	1963–64	[1] 54,800	15	39,600	72,500

[1] Includes 2,700 fish captured at the Idaho Power Company barrier net.

to leave the reservoir as age-group 0 fish in November 1963, and the emigration continued through June 1964 (fig. 4). Distinction between fish from the Weiser River and those from Eagle Creek was not always possible, but knowledge of the age of fish at the time of downstream migration to the reservoir provided a basis for their identification at certain times of the year. Krcma and Raleigh (1970) have shown that fish from the Weiser River do not enter the reservoir until spring 1 year after hatching, whereas fish from Eagle Creek enter at age 0 in the fall and again as age-group I in the spring. Spring chinook salmon that left the reservoir in the fall, winter, and early spring, therefore, were probably from Eagle Creek; fish leaving later in the spring and in early summer could be from either the Weiser River or Eagle Creek.

The emigration of the 1964 year class of spring chinook salmon was estimated at 14,000 fish, 51 percent of estimated immigration. Most of these fish were from Eagle Creek. Additional catches of juvenile migrants from Eagle Creek were made in the stream, transported downstream below Oxbow Dam, and released (Krcma and Raleigh, 1970). Juvenile spring chinook salmon that entered the reservoir in late March and early April 1964 migrated rapidly through the impoundment. Peak emigration was in mid-April, and the migration ended in late July (fig. 4).

Kokanee

The origin of, or reasons for, some migrations of juvenile kokanee into Brownlee Reservoir are not completely understood, but most fish observed during the present study were probably from the Payette River system (Payette Lakes and Cascade and Deadwood Reservoirs). Kokanee periodically migrate however, and rather large numbers of fingerlings entered Brownlee Reservoir in 1964

TABLE 8.—*Estimated immigration of juvenile native spring chinook salmon into Brownlee Reservoir from Eagle Creek and the Weiser River and estimated emigration from the Reservoir, November 1, 1963 to August 1965*

Year class	Estimated immigration			Years of emigration	Estimated emigration		Range of estimated emigration	
	Weiser River	Eagle Creek	Total				Low	High
	Number	*Number*	*Number*		*Number*	*Percent*	*Number*	*Number*
1963	15,000	22,300	37,300	1963–64	5,900	16	4,700	8,500
1964	6,800	7,200	14,000	1964–65	7,200	51	4,500	11,300

and 1965. In 1964, 2,100 kokanee fingerlings (1963 year class) were estimated to have left the reservoir, representing about 38 percent of the estimated recruitment to the reservoir (table 9). The outmigration started during the latter part of June 1964, reached a peak in early August, and ended by the first week in September.

TABLE 9.—*Estimated immigration of juvenile kokanee into Brownlee Reservoir from the Snake River system and estimated emigration from the Reservoir, May 1964 and 1965*

Year class	Estimated immigration	Year of emigration	Estimated emigration		Range of estimated emigration	
					Low	High
	Number		*Number*	*Percent*	*Number*	*Number*
1963	5,500	1964	2,100	38	1,700	2,900
1964	506,800	1965	52,100	10	4,200	73,200

An estimated half million age-group I kokanee entered Brownlee Reservoir in 1965, but only 10 percent (52,100 fish) are estimated to have left the reservoir. According to Durkin et al. (1970), the poor success of the migration of kokanee can be attributed to the high reservoir level and its attendant lack of downstream-orienting currents. These fish did not enter the reservoir until June and did not begin to leave until late June. The outmigration was greatest in late August and was completed by early September (fig. 5). Fish remaining in the reservoir in late July, August, and September were subjected to high temperatures in the epilimnion (above 21° C.) and oxygen-deficient water in the hypolimnion. These factors forced fish into unfavorable habitats where survival was poor (Durkin et al., 1970).

EMIGRATION OF JUVENILE HATCHERY-REARED SALMON

About 250,000 age-group 0 juvenile fall chinook salmon and 375,000 age I juvenile coho salmon were released in the Snake River above Brownlee Reservoir in late winter and early spring of 1964. Additional releases of 592,000 age-group 0 fall chinook salmon and 473,000 age-group I juvenile sockeye salmon were made in the spring of 1965. Chinook and coho salmon fingerlings were from hatcheries on the lower Columbia River; sockeye salmon fingerlings were from the Leavenworth National Fish Hatchery, where they had been reared from eggs obtained from Babine Lake in British Columbia.

Fall Chinook Salmon

About 85 percent (94,500) of the estimated 111,500 hatchery-reared juvenile fall chinook salmon that entered the reservoir in 1964 passed

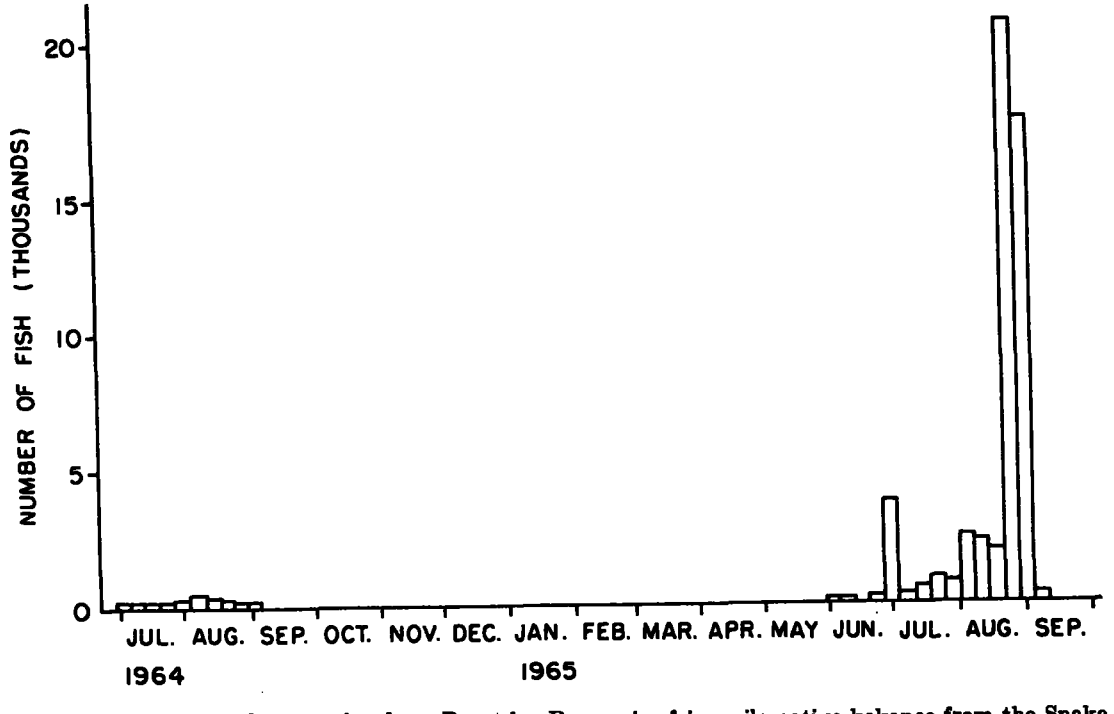

FIGURE 5.—Estimated emigration from Brownlee Reservoir of juvenile native kokanee from the Snake River system, 1964–65.

Brownlee Dam in 1964 (table 10). These fish first appeared at the traps below the dam in early April (9 days after release in the Snake River above the reservoir) and their numbers peaked in the second week of May. Small numbers of fish moved out of the reservoir through the summer until the emigration of the 1964 year class was completed on September 1 (fig. 6).

An estimated 275,200 hatchery-reared fall chinook salmon (1965 year class) left the impoundment in 1965—more than were estimated to have entered the reservoir. The discrepancy between the two estimates is probably due to different sampling methods. Nevertheless, such a comparison is useful when one recognizes that the low range emigration estimate (175,000 fish) is within the 95-percent statistical confidence range of the immigration estimate. Fish of the 1965 year class were first taken in the scoop traps below the dam in late March (fig. 6), 12 days after release in the Snake River above the reservoir. Peak migration was in mid-April, and a few fish were still leaving the reservoir when the experiment terminated at the end of August.

Coho Salmon

Emigration of juvenile hatchery-reared coho salmon (1963 year class) in 1964 was estimated at 51,600 fish or about 75 percent of immigration to the reservoir (table 11). The emigration of coho salmon began on May 16, 1964, about 6 weeks after their release in the Snake River above the reservoir. The run reached a peak 1 week later and continued until the end of August (fig. 7).

TABLE 10.—*Estimated immigration of juvenile hatchery-reared fall chinook salmon into Brownlee Reservoir from the Snake River and estimated emigration from the Reservoir, 1964–65*

Year class	Estimated immigration	Year of emigration	Estimated emigration		Range of estimated emigration	
					Low	High
	Number		*Number*	*Percent*	*Number*	*Number*
1964	111,500	1964	94,500	85	68,600	133,400
1965	162,800	1965	[1] 275,000	[1] >100+	175,000	432,000

[1] Discrepancy between estimates of immigration and emigration probably due to differences in sampling techniques in the Snake River and below Brownlee Reservoir.

Sockeye Salmon

Juvenile hatchery-reared sockeye salmon (1964 year class) released in 1965 had little difficulty in passing through the reservoir. Emigration in 1965 was estimated at 408,000 fish, more than 100 percent of the estimated immigration (table 11). The range of the two estimates overlap, however. The first sockeye salmon appeared in the scoop traps 6 days after the first releases on March 15, 1965. The emigration was relatively short, beginning on March 21 and ending by the second week of May (fig. 8). Peak was during the week of April 4 to 10, when 175,000 fish are estimated to have left the reservoir.

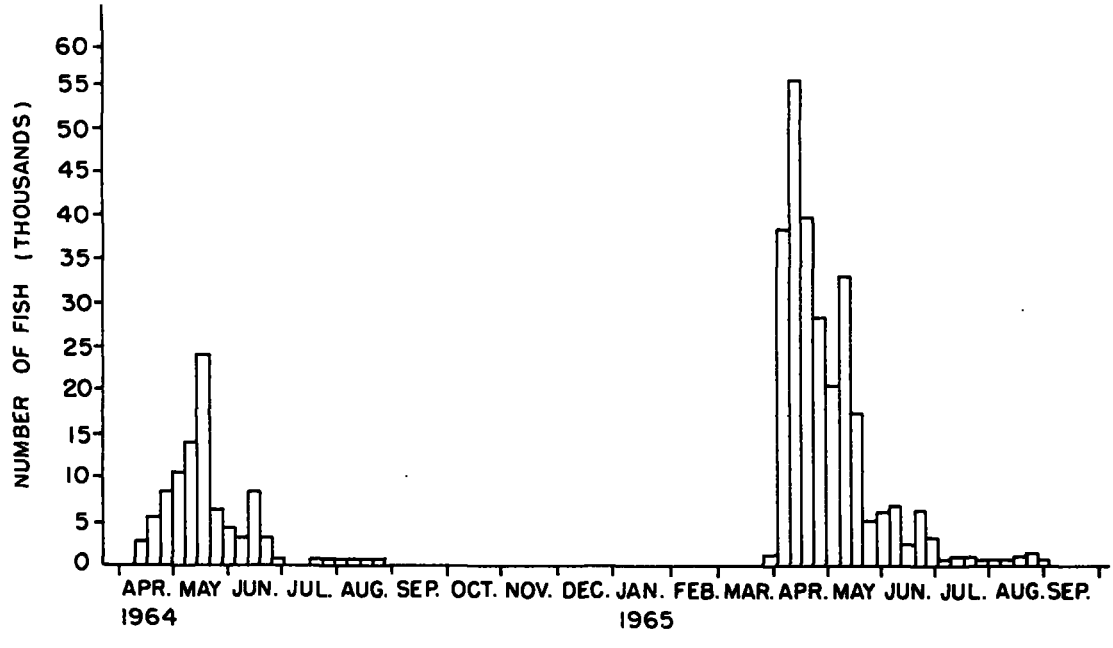

FIGURE 6.—Estimated emigration from Brownlee Reservoir of juvenile hatchery-reared fall chinook salmon from the Snake River, April 1964 to September 1965.

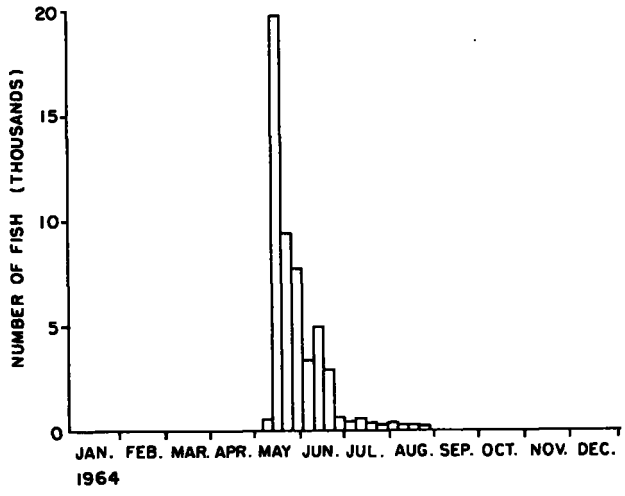

FIGURE 7.—Estimated emigration from Brownlee Reservoir of juvenile hatchery-reared coho salmon from the Snake River, 1964.

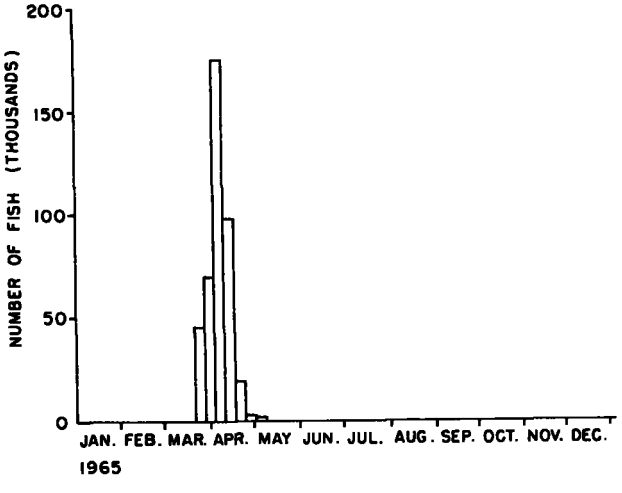

FIGURE 8.—Estimated emigration from Brownlee Reservoir of juvenile hatchery-reared sockeye salmon from the Snake River, 1965.

TABLE 11.—*Estimated immigration of juvenile hatchery-reared coho and sockeye salmon into Brownlee Reservoir from the Snake River and estimated emigration from the Reservoir, May 1, 1963 to August 31, 1965*

Year class	Species	Estimated immigration	Year of emigration	Estimated emigration		Range of estimated emigration	
						Low	High
		Number		*Number*	*Percent*	*Number*	*Number*
1963	Coho	69,000	1964	51,600	75	37,900	72,600
1964	Sockeye	360,000	1965	[1] 408,000	[1] >100+	324,000	513,500

[1] Discrepancy between estimates of immigration and emigration probably due to differences in sampling techniques in Snake River and below Brownlee Reservoir.

EMIGRATION OF JUVENILE TROUT OF UNKNOWN ORIGIN

Because anadromous rainbow trout (steelhead) could not be separated from native and hatchery-reared resident rainbow trout, the data on emigration include all populations of rainbow trout. For the same reason, Krcma and Raleigh (1970) did not attempt to estimate immigrations of rainbow steelhead trout. Comparisons of emigration and immigration, therefore, were not possible. Juvenile rainbow trout emigrated from Brownlee Reservoir each year during this study. An estimated 24,800 rainbow-steelhead trout (table 12) left the reservoir from August 1963 through December 1964. The major emigrations were in May and June. In 1965, emigration was estimated at 73,600 fish, and the major outmigrations were in April and May.

TABLE 12.—*Estimates of emigration of juvenile native and hatchery-reared resident rainbow trout and anadromous rainbow (steelhead) trout from Brownlee Reservoir, May 1, 1963, to August 31, 1965*

Year of emigration	Estimated emigration	Range of estimate	
		Low	High
	Number	*Number*	*Number*
1963–64	24,800	17,900	35,000
1965	73,600	46,600	116,000

LENGTHS OF EMIGRANTS

The sizes of the juvenile fish in various stocks that emigrated from Brownlee Reservoir generally increased as the season progressed. The fork length of fall chinook salmon caught below the dam from August 1963 through December 1964 was 45 to 240 mm. (table 13). Two distinct length groups were evident from November 1963 through June 1964. The larger fish (age-group I) were from the 1963 year class of fall chinook salmon from the Snake River; these fish dominated the catch through March 1964. Beginning in April 1964, the smaller native spring chinook salmon of the 1963 year class and the hatchery releases of fall chinook salmon of the 1964 year class dominated. Holdover of fish was slight in 1965; the entire emigration was of native kokanee and spring chinook salmon (age-group I) of the 1964 year classes and hatchery releases of sockeye salmon (age-group I) and fall chinook salmon (age-group 0) of the 1964 and 1965 year classes.

Hatchery-reared coho salmon increased from an average length of 125 mm. (90–155 mm.) in May 1964 to 200 mm. (155–245 mm.) in August 1964 (fig. 9).

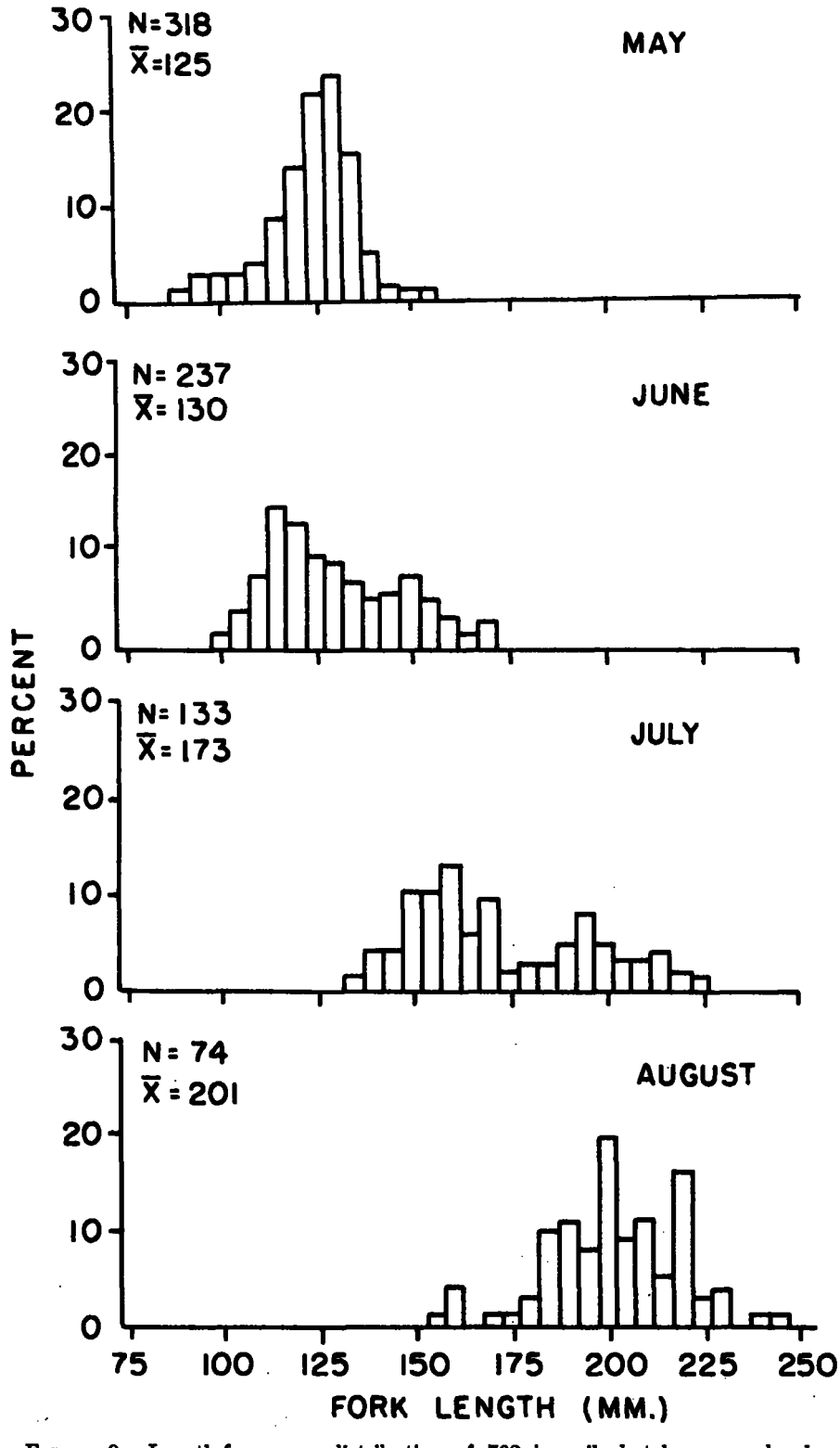

FIGURE 9.—Length-frequency distribution of 762 juvenile hatchery-reared coho salmon from the Snake River collected below Brownlee Dam, May 16 to August 31, 1964. (N=number of fish; $\bar{X}$ indicates average length.)

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TABLE 13.—*Length-frequency distribution of 5,697 juvenile fall chinook salmon from the Snake River collected below Brownlee Dam, August 1, 1963 to August 31, 1965*

Fork length	Number of fish by year and month											
	1963					1964						
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
Mm.												
240												
235												
230								1				
225								3	4			
220							2	13	6	1		2
215						7	8	29	16	2		3
210					1	13	25	49	25			3
205					1	41	47	45	24			2
200					7	48	55	34	10	1		1
195			1	2	13	43	26	17	9	2		
190				12	14	23	21	15	6	2		1
185				21	22	12	4	7	7	1		2
180			1	13	7	5	6	4	6	1		4
175			1	13	2	2		4	3			3
170	1	1		2	1	3	4	3				8
165	3	2	3	3	1	1	3	2				3
160	8	3	1	2			1	3				6
155	13	4	2									7
150	36	8								2	1	2
145	42	2								4	2	2
140	15								1	14	4	2
135	4							1	4	37	1	
130	1				1		1	4	11	86	16	
125	1				3	3	4	7	7	89	52	
120					2	3	6	10	12	66	111	
115					14	5	9	13	28	58	158	
110					7	3	12	15	50	65	131	
105					4	6	8	32	45	62	58	
100					2	1	10	29	51	76	20	
95				1	5		2	15	55	55	12	
90					1		4	6	56	43	1	
85							2		68	44	1	
80							2		74	32		
75									104	21		
70				1					102	8		
65									98	1		
60									31			
55									19			
50									1			
45									1			
Total	124	20	9	70	108	219	262	361	934	773	568	51

The average lengths of kokanee differed little in the early and late runs in 1964 (about 5 mm.), but in 1965 the average increased from 105 to 138 mm. during a 90-day period in June, July, and August (fig. 10).

Hatchery-reared sockeye salmon migrated through the reservoir during such a short period in 1965 that size of the fish changed little. The lengths of these fish were 75 to 170 mm. (fig. 11).

Length-frequency distributions for juvenile rainbow-steelhead trout are given in table 14. Lengths of trout below the dam were 65 to 368 mm. The larger fish probably were native rainbow trout rather than the offspring of anadromous steelhead trout.

EFFECT OF ENVIRONMENT ON EMIGRATION

The environment significantly affected the passage of juvenile salmon and trout through Brownlee Reservoir. In 1963, emigration from the reservoir was low when (1) reservoir drawdown in the spring was small, (2) the reservoir was filled early, and (3) maximum discharge was late.

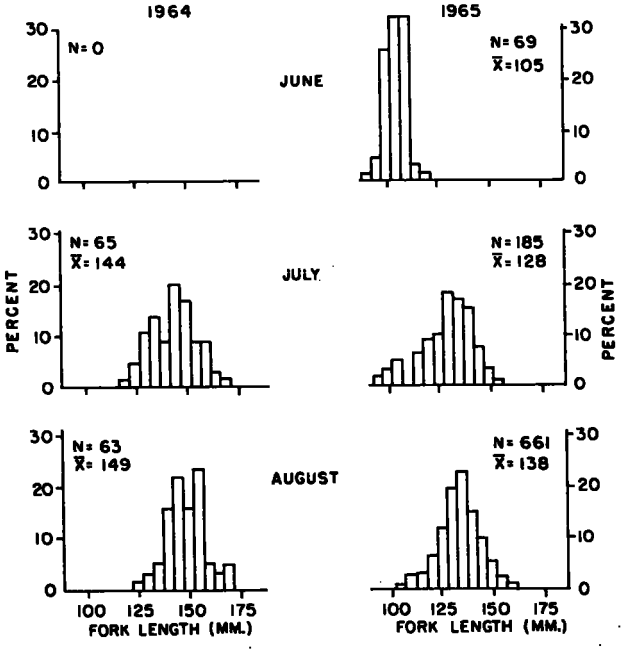

FIGURE 10.—Length-frequency distribution of 1,043 juvenile native kokanee from the Snake River collected below Brownlee Dam, 1964 and 1965. (N=number of fish; $\bar{X}$ indicates average length.)

TABLE 14.—*Length-frequency distribution of 1,381 juvenile rainbow-steelhead trout collected below Brownlee Dam, August 1, 1963 to August 31, 1965*

Length (mm.)	Number of fish by year and month											
	1963					1964						
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
350-359												
340-349											1	
330-339						2			1	1	2	1
320-329						2		1	3	1		
310-319						2		4	2	4	1	
300-309						4	5	8	14	5	1	
290-299	1			1		1	5	6	2	3		
280-289						1		1	1	2	2	
270-279								3				1
260-269	2								1		1	1
250-259			1							4		6
240-249	2	1							1	1		11
230-239	4							1	1	11		9
220-229	1							1	1	3	5	8
210-219								1	5	9	7	4
200-209								1	2	12	21	6
190-199								1	6	13	13	
180-189								1	2	19	15	1
170-179				1					9	29	7	
160-169							1	1	13	22	1	
150-159						1			14	15	1	
140-149									11	14		
130-139									9	8		
120-129									3	1		
110-119						1			3		1	
100-109									2	1		
90-99												
80-89									2		1	
70-79									2			
60-69												
Total	10	1	1	2	0	14	11	30	110	178	80	48

TABLE 14.—*Length-frequency distribution of 1,381 juvenile rainbow-steelhead trout collected below Brownlee Dam, August 1, 1963 to August 31, 1965*—Continued

Length (mm.)	Number of fish by year and month											
	1964					1965						
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
360-369									1		1		
350-359	1								1				
340-349								1	1	1			
330-339	2								2				
320-329			1							2	2	1	1
310-319								1	3	1	1		1
300-309								2	1				3
290-299	1							1	3	2			12
280-289	2							1	1	4	1		10
270-279	4								3	9	2		13
260-269	6							1	8	7	3	5	24
250-259	12							1	18	12	2	8	17
240-249	11								24	16	3	5	16
230-239	3	2						1	32	20	1	5	8
220-229	4								24	18	5	3	
210-219	1								34	17	7		2
200-209		1							19	18	5		
190-199									22	30	12	1	
180-189	1		1						32	25	15	2	
170-179				1					43	26	18		
160-169								1	27	22	11		
150-159									13	14	5		
140-149				1				1	9	4	1		
130-139					1				3	4	1		
120-129						1			1		3		
110-119										1	2		
100-109				1		1							
90-99			1						1			1	3
80-89			1							1			3
70-79													
60-69								1					
Total	48	3	4	3	1	2	0	12	326	254	99	31	113

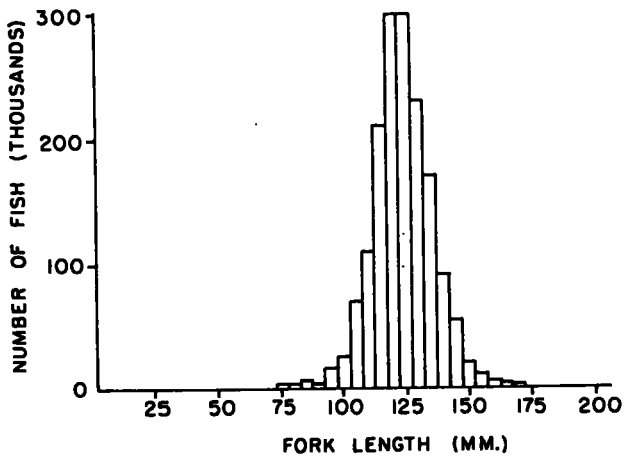

FIGURE 11.—Length-frequency distribution of 1,626 juvenile hatchery-reared sockeye salmon from the Snake River collected below Brownlee Dam, March 21 to May 13, 1965.

Emigration was notably more successful in 1964 and 1965 when the reservoir level was low through most of the downstream migration, and discharges were high during early and midspring.

Fish that entered the reservoir after the middle of June, as kokanee did in 1964 and 1965 (fig. 5), had poor success of passage. In both years, emigration of kokanee was less successful than that of other species of fish migrating earlier in the season. Kokanee did not enter the reservoir until late June when the reservoir was full and currents were weak and not clearly oriented in any direction. Those fish remaining in the reservoir through the summer encountered low oxygen concentrations (0–3 p.p.m.) below the thermocline and high water temperatures (24° C. or above) near the surface (Ebel and Koski, 1968). Few kokanee survived the harsh summer.

MORTALITY RELATED TO TURBINES

Because many fish were found dead in the scoop traps, the mortality attributable to the traps and the turbines was examined. A detailed investigation was beyond the scope of this study, but mortality was assessed at the turbine tailrace site in June 1965. During a 6-day period (June 1–6), all scoop traps were emptied twice daily—at 8:00 a.m. and 4:00 p.m. In a second 6-day period (June 7–12), all fish were removed as soon as they entered the traps (table 15). All fish caught during both periods were hatchery-reared chinook salmon of the 1965 year class.

Mortality during the two periods was as indicated in table 15: 88 percent of the fish were dead in the traps in the first period, and 16 percent were dead when they entered the traps in the second period. Because the fish were removed immediately in the second period, they died of causes other than trapping or handling.

To assess delayed mortality, samples of live fish taken from the traps during the second period were held in a holding tank in circulated water for an additional 24-hour period. Hatchery-reared chinook fingerlings collected in the reservoir above the dam were held with these fish to serve as a control (table 16). At the end of 24 hours, 67.5 percent of the fish taken from the traps and 17.5 percent of the control fish were dead. Thus, the delayed mortality of fish passing through the turbines was 50 percent.

Thus, on the average under test conditions, 16 of every 100 fish passing the sampling site were already dead. Of the 84 survivors, 42 died within 24 hours, which indicated a total turbine-related mortality of 58 percent.

TABLE 15.—*Mortality of juvenile hatchery-reared chinook salmon taken by scoop traps at the turbine tailrace sampling site, June 1–12, 1965*

Date	Turbine discharge	Water temperature	Fish in total catch	Mortality	
	M.³/sec.	*°C.*	*Number*	*Number*	*Percent*
Period A:[1]					
June 1	451	13	105	66	62
June 2	484	13	83	77	93
June 3	478	15	167	160	96
June 4	470	15	230	216	94
June 5	472	14	160	146	91
June 6	410	15	323	274	85
Totals			1,068	939	88
Period B:[2]					
June 7	547	15	148	26	18
June 8	523	15	65	12	19
June 9	440	15	23	1	4
June 10	433	15	18	1	5
June 11	423	16	4	1	25
June 12	334	17	15	2	13
Totals			273	43	16

[1] Normal operating conditions. Trap emptied at 8:00 a.m. and 4:00 p.m. daily.
[2] Fish removed from trap immediately upon entry.

TABLE 16.—*Delayed mortality of juvenile hatchery-reared chinook salmon taken from the tailrace scoop traps, June 7–12, 1965*

Group	Fish in trap	Mortality at the end of 24 hours	
	Number	*Number*	*Percent*
Experimental	83	56	67.5
Control	103	18	17.5

SUMMARY AND CONCLUSIONS

Estimates of emigration of juvenile salmon and trout from Brownlee Reservoir from July 1963 through August 1965 were based on catches in floating scoop traps below Brownlee Dam and on estimates of efficiency of the traps.

Emigration of native fall chinook salmon of the Snake River was estimated at 15 percent of immigration into the Reservoir in 1963 (1963 year class). Hatchery-reared fall chinook salmon (age-group 0) were planted in the Snake River in 1964 and 1965. Estimates of emigration were 85 percent of immigration in 1964 and 100 percent in 1965.

Emigration of native spring chinook salmon (Eagle Creek and the Weiser River) was estimated at 16 percent of immigration in 1964 and at 51 percent in 1965.

Emigration of native kokanee of the Snake River system was estimated at 38 percent of immigration in 1964 and at 10 percent in 1965.

Hatchery-reared coho and sockeye salmon were planted in the Snake River in 1964 and 1965, respectively. An estimated 75 percent of the coho salmon (1963 year class) that entered the reservoir in 1964 passed through. Emigration of sockeye salmon (1964 year class) in 1965 was estimated at 100 percent of immigration.

Because anadromous rainbow trout (steelhead) could not be separated from populations of native and hatchery-reared resident rainbow trout, I did not compare emigrations and immigrations. About 24,800 rainbow trout left the reservoir from August 1963 through December 1964. Emigration was estimated at 73,600 fish in 1965.

The environment in the reservoir during the time of outmigration clearly affected success of passage. In general, fish that entered the reservoir early in the spring, when the reservoir was drawn down and water temperature and oxygen concentrations were favorable, passed through more successfully than did those that entered during the summer, when water temperatures were high, currents were weak, and concentrations of oxygen were low.

The fish of the various stocks that emigrated from Brownlee Reservoir showed a general increase in length as the season progressed.

The following general conclusions were reached:

1. Downstream migrants that entered the reservoir early in the season passed through more successfully than those that entered later.
2. Emigration was more successful when the reservoir level was low during the time of migration than when the reservoir was filled before completion of the migration.
3. Because of time of emigration, size of the fish at time of entry into the reservoir, and the shorter distance traveled by the fish, one would expect what happened: Progeny of native spring chinook salmon migrated through the reservoir more successfully than native fall chinook salmon.

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CHARACTERISTICS OF SOME LARVAL BOTHID FLATFISH, AND DEVELOPMENT AND DISTRIBUTION OF LARVAL SPOTFIN FLOUNDER, *CYCLOPSETTA FIMBRIATA* (BOTHIDAE)[1]

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ABSTRACT

Pertinent literature on larval flatfish of the family Bothidae and some of the characters helpful in identifying these larvae are discussed. Helpful characters are of two types; transitory, those which are lost, and permanent, those which are retained. Transitory characters include larvae pigmentation, elongate dorsal and pelvic fin rays, and spination; permanent characters include meristic counts, placement of pelvic fin bases and fin rays, and caudal osteology.

Developmental changes in general growth patterns, formation of fins, larval spination, pigmentation, migration of the right eye, and sequence of ossification based on 171 larvae (1.7–14.5 mm. SL) collected off the south Atlantic coast of the United States is presented. Several sizes of larvae showing spination, pigmentation, and elongate fin rays are illustrated, and one illustration shows the degree of ossification.

Spawning appears to occur between April and October in waters of about 50 m. or less. Fertilized eggs have not been seen, but their size at hatching is estimated to be about 1.5 mm.

Five families of flatfish occur off the southeastern coast of the United States (Bothidae, Scophthalmidae, Pleuronectidae, Soleidae, and Cynoglossidae). Species of bothids are common in the inshore waters south of Cape Hatteras, N.C., and are more numerous (13 genera and 49 species) than are species of the other four families (Cynoglossidae, 1 genus and about 15 species; Soleidae, 3 genera and 5 species; Pleuronectidae, 1 genus and 3 species; Scophthalmidae, 1 genus and 1 species).

The spotfin and other flounders discussed in this paper are taken in industrial fish catches or are caught incidentally in shrimping. Of these flounders, only the fluke (*Paralichthys*) is removed from the catch and its flesh utilized. Flukes are also fished for sport or commercially along much of the east and Gulf coasts of the United States. Several other species of large flounders may be fished commercially in the future if stocks of sufficient size can be found.

Larvae of flatfish along the southeastern coast of the United States are poorly known; however, a few authors have illustrated and described some of these fish taken off North Carolina. Goode and Bean (1896) identified an *Ancylopsetta dilecta* larvae (listed as *Notosema dilecta*, Bothidae); Hildebrand and Cable (1930) had larvae of *Paralichthys* (Bothidae); and Deubler (1958) showed the postlarvae of *Paralichthys*. Hildebrand and Cable illustrated and described larvae of *Symphurus plagiusa* (Cynoglossidae) in 1930, and the larvae of *Trinectes maculatus* (listed as *Achirus fasciatus*, Soleidae) in 1938 from off North Carolina.

I discuss the literature pertaining to the larvae of *Syacium* (Bothidae) in some detail, because of the many similar external features between the larvae of *Cyclopsetta* and *Syacium*. Both genera have many elongate dorsal and pelvic fin rays, a single sphenotic spine, and heavy preopercular spines, but larvae of *Cyclopsetta* have more numerous elongate dorsal fin rays, and the sphenotic and preopercular spination is smaller.

This paper reports on development of larvae of spotfin flounder, *Cyclopsetta fimbriata*, that U.S. Fish and Wildlife Service vessels *Theodore N. Gill* and *Oregon* collected off the south Atlantic coast of the United States (fig. 1). It describes growth changes in the head length, body depth, eye diameter, snout length, and upper and lower

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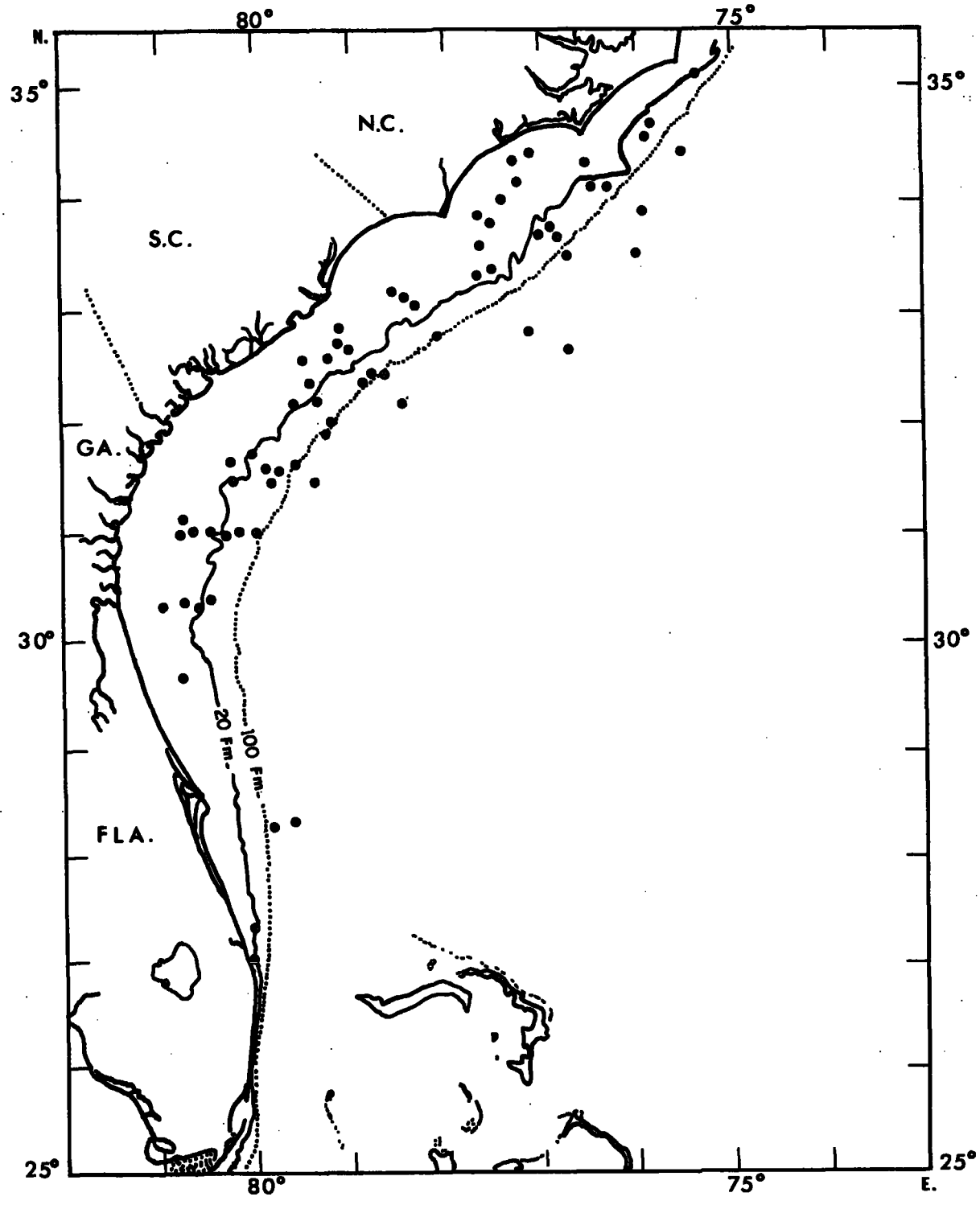

FIGURE 1.—Collection sites of *Cyclopsetta fimbriata* larvae from cruises of U.S. Fish and Wildlife Service vessels *Gill* and *Oregon*.

jaw lengths, and the development of fins, spination, pigmentation, sequence of ossification, and migration of the right eye.

REVIEW OF PERTINENT LITERATURE CONCERNING BOTHID LARVAE

In their description of *Ancylopsetta dilecta* (three-eyed flounder), Goode and Bean (1896) did not mention the larva they illustrated or any of its larval characters. The following characters are taken from the illustration: about 70 dorsal fin rays, the 9 anteriormost elongate; about 60 anal fin rays; 6 pelvic fin rays, the first three are elongate and extend almost to the caudal peduncle; ocular-side pelvic fin on median line; small eye; large mouth; origin of dorsal fin anterior to anterior edge of eyes; migrating (right) eye appears to move under the dorsal fin or through the head. All of these characters except the number of fin rays are present on large larvae of *Cyclopsetta*. Well-developed preopercular spines and a single sphenotic spine are present on larval *Cyclopsetta* but are not shown on Goode and Bean's illustration. Despite the lack of spines on their illustration, I believe their specimen is a *Cyclopsetta*.

In *Ancylopsetta*, the ocular-side pelvic fin is above the median line; the origin of the dorsal fin is above the anterior part of the eye, not in advance of it; the eyes are large, and the right side eye probably migrates over the median dorsal ridge anterior to the origin of the dorsal fin, not under it. I do not know if larvae of *Ancylopsetta* have elongate dorsal and pelvic fin rays.

Many species of Bothidae have elongate dorsal and pelvic fin rays in the larval stage, but larvae of *Syacium* are the only other bothid larvae to have numerous elongate dorsal (more than five) and pelvic (generally three) fin rays. *Symphurus* larvae (family Cynoglossidae) also have elongate dorsal rays, that can number up to seven. The numbers of dorsal and anal fin rays that Goode and Bean (1896) show are too low for *Syacium*, and the elongate pelvic fin rays they show are too long for *Syacium*.

I am unaware of any published accounts of *Ancylopsetta* larvae except those in which *Syacium*, *Cyclopsetta*, *Citharichthys*, or *Etropus* larvae have been misidentified as *Ancylopsetta*. Kyle (1913) described and illustrated (fig. 27) a 6- to 7-mm. larva he called *Ancylopsetta* sp. Regan (1916) illustrated (plate 9, fig. 3) a specimen identified as *A. quadrocellata* that he said resembles Kyle's (1913) *Ancylopsetta;* Regan's second illustration (plate 9, fig. 4) is a 4-mm. larva that he called *Ancylopsetta* sp. Both of Regan's (1916) larvae as well as the larva figured by Kyle (1913) are larvae of *Syacium*. Aboussouan (1968) discussed in detail the relation of Kyle's (1913) *Ancylopsetta* and Regan's (1916) *Ancylopsetta* to *Syacium*. Dannevig (1919) and Hsiao (1940) recorded *Ancylopsetta* larvae from eastern Canada and along the outer edge of Georges Bank that are similar to Kyle's *Ancylopsetta* sp. and these also are larvae of *Syacium*—warm-water species of vertebrates and invertebrates in this area are not uncommon (Bigelow, 1926, and Colton, 1961). Pearson (1941) listed *Ancylopsetta* sp. in plankton collections from Chesapeake Bay, but these are probably *Etropus* or *Citharichthys*. Pearson (1941: 84) stated, "The most characteristic features of the two fish are the pronounced elongation of the first two dorsal rays, the latter reaching nearly a quarter the length of the body, and the elongation of one of the ventral fins into a filament extending to the vent." These larval characters are found on larvae of *Etropus* and *Citharichthys*, and species of these two genera are known from Chesapeake Bay. *Cyclopsetta* and *Syacium* have not been reported north of Cape Hatteras, N.C., except for larvae of *Syacium* referred to as *Ancylopsetta* by Dannevig (1919) and Hsiao (1940).

Known larvae of *Etropus* have 2 elongate dorsal fin rays, and *Citharichthys* larvae have 0 to 3 elongate dorsal fin rays (5–10 in *Cyclopsetta* and *Syacium*) and 1 or 2 elongate pelvic fin rays (3 in *Cyclopsetta* and *Syacium*).

S. guineensis (Bleeker, 1862) probably is a synonym of *S. micrurum* Ranzani 1840; if so, the larvae described by Aboussouan (1968) from off Dakar are those of *S. micrurum*. Norman (1934) listed *S. guineensis* in the synonymy of *S. micrurum* and gave its distribution as "Atlantic coast of tropical America from Florida to Rio de Janeiro, tropical West Africa." Distinguishing between adult *S. guineensis* and *S. micrurum* is difficult, and they are separated by their distribution; *S. guineensis* off west Africa and *S. micrurum* off Florida, the Antilles, through the Gulf of Mexico and the Caribbean Sea, and off the Atlantic coast of South America to Rio de Janeiro.

Three species of *Syacium* occur in the western North Atlantic. *S. papillosum* (Linnaeus, 1758) and *S. micrurum* are difficult to separate as juveniles and can be separated as adults only by the width of the interorbital space. All other meristic and morphometric characters overlap. *S. gunteri* Ginsburg, 1933 can usually be separated from the other two species of *Syacium* in the western North Atlantic by the number of dorsal and anal fin rays. *Syacium papillosum* and *S. micrurum* rarely have fewer than 85 dorsal fin rays or fewer than 68 anal fin rays, whereas *S. gunteri* rarely has more than 84 dorsal fin rays and more than 67 anal fin rays (Gutherz, 1967).

Aboussouan's (1968) description of larval *S. micrurum* (listed as *S. guineensis*) is of greatest value for workers in the area off Dakar where only one species of *Syacium* is known. His paper is valuable in separating *Syacium* larvae from the larvae of other genera.

Aboussouan (1968) implied that Kyle's *Citharichthys* B. (Kyle, 1913; fig. 29) is a *Syacium* rather than a *Citharichthys*, but I disagree for the following reasons: At this stage of development larvae of *Syacium* have numerous elongated dorsal and pelvic fin rays but the known larvae of *Citharichthys* have only a few, if any, elongate fin rays; *S. gunteri* has fin ray counts similar to those given by Kyle for *Citharichthys*, but our larvae of *S. gunteri* have the heavy preopercular spination and the large sphenotic spine seen on the larvae of the other species of *Syacium;* the preopercular armature of *Syacium* is not reduced or blunted until the right side eye has reached the middorsal ridge or is turning onto the left side; the mouth of *Syacium* larvae is larger than that shown by Kyle, and the origin of the dorsal fin is more anterior; the larvae of several species of bothids have pigment patterns similar to *Citharichthys* B. I believe this specimen probably represents a *Citharichthys* or *Etropus*.

Paralichthys sp. and *P. olivaceous* larvae have been figured and described by Hildebrand and Cable (1930); Deubler (1958); Chang, Xo, and Sha (1965); and Okiyama (1967). These descriptions are based on larvae collected off the Atlantic coast of the United States, off Japan, and on laboratory-reared specimens. A high degree of similarity in the developmental pattern is noted except for Okiyama's *P. olivaceous*, which have longer elongate dorsal fin rays that seem to persist longer than the elongate dorsal fin rays on the larvae described by Chang et al. (1965). Characteristics common for the eggs and larvae of *Paralichthys* and a discussion of the relation between the migrating eye and the anterior portion of the dorsal fin are given by Chang et al. (1965).

Hippoglossina oblonga larvae have been illustrated and described by Agassiz (1879, listed as *Pseudorhombus oblongus*), Perlmutter (1939), and Miller and Marak (1962, listed as *Paralichthys oblongus*).

Citharichthys larvae have been figured by Ahlstrom (1965), and Kyle (1913, fig. 29) has illustrated what is probably a *Citharichthys* or *Etropus*.

Bothus larvae have been illustrated and described by Kyle (1913), Colton (1961), and Ochiai and Amaoka (1963) among others. These descriptions and figures of larvae collected off the Atlantic coast of the United States, the mid-Atlantic region, and off the Japanese coast show a high degree of similarity. All have only one elongate dorsal ray.

Chascanopsetta larvae have been illustrated and described by Kyle (1913) and Bruun (1937). Kyle was unable to refer his larva to any known Atlantic species, but Bruun placed it in *Chascanopsetta*.

Illustrations and descriptions of larvae in the closely related Scophthalmidae can be found in Smith (1904), Moore (1947), and Bigelow and Schroeder (1953).

MATERIALS AND METHODS

The original sampling procedures used on cruises of the FWS (U.S. Fish and Wildlife Service) vessel *Theodore N. Gill* were reported by Anderson, Gehringer, and Cohen (1956) and Anderson and Gehringer (1957).

Additional plankton samples were collected in January and June 1967 on cruises of the FWS vessel *Oregon*. Plankton and nekton samples were collected in depths of 14.6 to 45.7 m. (8–25 fath.) by 1-m. plankton and nekton nets (1-mm. mesh) and ½-m. plankton nets (1-mm. and 0.33-mm. mesh), which were towed for 15-minute periods.

A size series of specimens was cleared and stained by the procedure given by Taylor (1967).

All measurements were made with an eyepiece micrometer and a stereoscopic microscope and recorded to the nearest 0.01 mm.

MEASUREMENTS

Measurements used when working on larval flatfish require definition, because they differ significantly from those used on adult flatfish.

Standard length (SL) : Tip of snout to that point on notochord where dorsal flexture takes place (dorsal and anal finfolds have a slight indentation where the notochord turns dorsally, actinotrichia are visible in the caudal region of the finfold immediately posterior to this indentation) ; or tip of snout to base of median caudal fin rays if these rays are developed; or tip of snout to distal end of hypurals if caudal fin rays are developed.

Head length (HL) : Tip of snout to posterior edge of cleithrum on a horizontal line through center of left eye on small larvae; or tip of snout to origin of dorsalmost part of pectoral fin base; or tip of snout to posteriormost part of opercle on large larvae.

Body depth (BD) : When left side pelvic fin base is not developed, vertical depth is taken immediately posterior to the cleithrum; or from origin of left side pelvic fin base to dorsal margin of body (excluding finfold or rays).

Origin of pelvic fin base to cleithrum: Least distance from origin of pelvic fin base to ventral tip of cleithrum, both left and right sides.

Eye diameter (ED) : Horizontal distance across the left eye.

Upper jaw length (UJL) : Anterior tip of premaxillary to distal edge of maxillary.

Lower jaw length (LJL) : Symphysis of lower jaw to posterior edge of angular.

Snout length (SN) : Anteriormost part of premaxillary to anterior edge of left eye.

COUNTS

Dorsal, anal, caudal, and pelvic fin rays: Total number of fin rays in which the basal portion is distinguishable.

PROBLEMS ENCOUNTERED IN WORKING WITH LARVAL FLATFISHES

The wide variation in measurements and counts of larval flatfishes may be due to distortion by preservation or to differing rates of development. When killed and preserved the larvae often curl; the pectoral fins may harden in an extended position; the mouth may open and distort some head features; and the eyes often distend, shrink, or fall out. Larval fish are fragile, and fin rays are often broken, particularly the elongate rays. Poor preserving and collecting techniques often damage or distort specimens. Fresh, well-preserved, flatfish larvae can be held in place for examination by a cover slide, but older, softer, or poorly preserved material may be damaged if handled in this manner. Older, softer specimens are often difficult to measure; however, they are often partially or completely bleached, so that the fin rays and myomeres or vertebrae are easier to count than in the fresh firmer specimens. Much of the material from the *Theodore N. Gill* is soft, but that from more recent *Oregon* cruises is in excellent shape.

Pigment patterns fade and are lost in preservative, so a knowledge of when specimens were collected is important; also the rate of development is not the same for all individuals. Larvae collected over a wide geographic area and an extended period of time may show differing rates of development. Within a species, fishes that metamorphose at small sizes probably have different rates of development from those that metamorphose at larger sizes. These differences must be recognized when working with larval flatfish.

CHARACTERS USEFUL IN IDENTIFYING BOTHID LARVAE

Characters that can be used to identify bothid larvae fall into two categories: (1) transitory, those which are present during part or all of the larval period but eventually are lost and (2) permanent, those which develop during the larval period and are retained in the juvenile and adult stages.

Transitory characters include larval pigmentation, elongate fin rays, and head and body spination. Type and intensity of these transitory characters may be of generic or specific significance. Many of the bothid genera in the western North Atlantic have elongate dorsal and pelvic fin rays in the larval stages: *Paralichthys* (Hildebrand and Cable, 1930) ; some *Citharichthys* (Ahlstrom, 1965; *C. stigmaeus* has no elongate dorsal fin rays) ; *Syacium* (Aboussouan, 1968) ; *Bothus* and

Chascanopsetta (Kyle, 1913); and *Cyclopsetta* (Goode and Bean, 1896). Many bothid larvae in the western North Atlantic have spines. These are more frequently seen on the preopercular margin than on the head or body. Most bothids have a swim bladder during the larval stage. Those larvae with a protracted larval stage retain the swim bladder longest. The migrating eye moves over the middorsal ridge anterior to the origin of the dorsal fin or through the head between the dorsal fin and the supraorbital bars of the cranium.

Permanent characters include meristic counts, relation of the origin of the pelvic fin bases to each other and to the cleithrum, and the arrangement of the caudal fin rays with respect to the other caudal fin rays and the bones of the hypural plate. Size at metamorphosis is important in distinguishing between genera.

MERISTIC CHARACTERS

The most important characters for identification of bothid larvae are meristics. Myomeres, which correspond in number to vertebrae, are the first countable item to develop. Those near the anterior and posterior portions of the body are difficult to count in the early stage larvae. Abdominal vertebrae usually number 10, but can be 11 (*Chascanopsetta* has 16 or 17). Caudal vertebrae are much more variable, ranging from 23 to 42. The vast majority of bothid larvae have between 34 and 40 total vertebrae or myomeres. Dorsal and anal fin ray numbers are also variable and overlap widely between species of Bothidae. The adult complements of dorsal and anal fin rays are distinguishable in larval *C. fimbriata* by about 8-mm. SL (fig. 2). The rate of fin ray development and the fin ray numbers at the various sizes may have generic or specific value. Although much meristic overlap is evident among species of bothids, several species can be separated by meristic values.

PELVIC FIN

Pelvic fin characteristics helpful in determining a genus or generic group are: the position of the fin bases in relation to the median line, size of larvae when the left fin base and rays first appear, relation of the origins of the right and left side fin bases to the cleithrum, and the number of elongate fin rays.

Four of the 13 genera of bothids in the western North Atlantic (*Paralichthys*, *Ancylopsetta*, *Gastropsetta*, and *Hippoglossina*) have the left and right side fin bases above the median line; all other western North Atlantic bothid genera have the left side fin base on the median line and the right side fin base above the median line.

I have only seen *Paralichthys* of the four genera with left and right side pelvic fin bases above the median line. In *Paralichthys* the left side fin base does not appear until the larvae are about 7 mm.

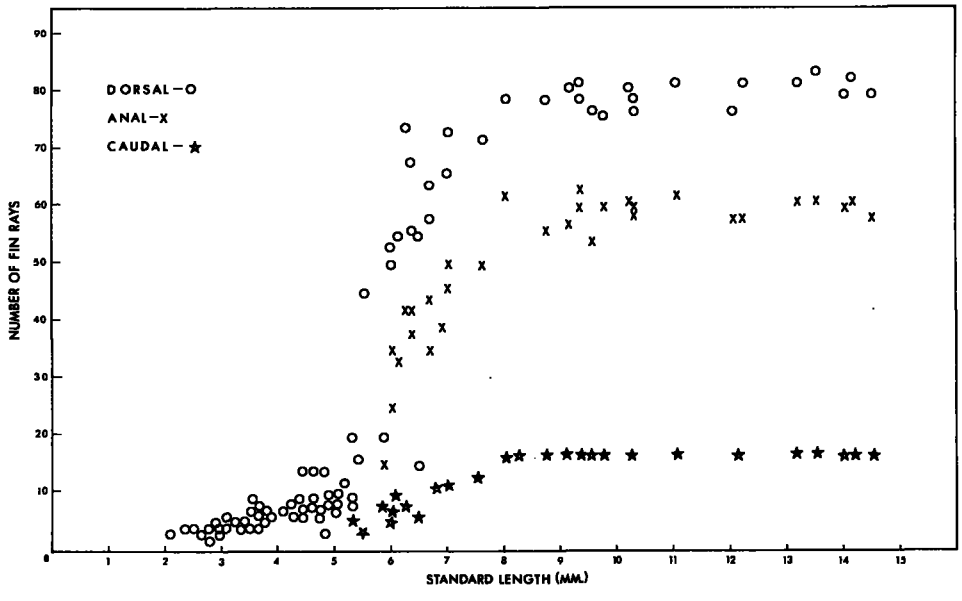

FIGURE 2.—Relation of number of dorsal, anal, and caudal fin rays to standard length of *Cyclopsetta fimbriata* larvae.

SL. I have not seen the larvae of *Ancylopsetta*, *Gastropsetta*, or *Hippoglossina*, but an illustration of a 5.7–mm. SL *Hippoglossina oblongus* by Perlmutter (1939); and illustrations of a 6.5–mm. specimen and a larger one by Agassiz, (1879, plate 9, figs. 4 and 5) do not show a left side pelvic fin. The pelvic fins of *H. oblongus* appear very much later than do the dorsal and anal fins (Agassiz, 1879).

At 5 mm. SL *Syacium*, *Cyclopsetta*, *Citharichthys*, and *Etropus* have a well-developed pelvic fin on the left side. The left side fin base appears at 2 to 3 mm. SL and is better developed than the right side base, which develops later.

I do not know at what size the pelvic fin bases first appear in *Engyophrys*, *Trichopsetta*, or *Monolene* (I have assigned larvae exceeding 8 mm. SL with well-developed pelvic fin bases to *Engyophrys* and *Monolene*). The origin of the left side fin base of adults is adjacent to the cleithrum or slightly anterior to it in *Engyophrys*, *Trichopsetta*, and *Monolene*, but the origin of the right side fin base is slightly posterior to the cleithrum.

The origins of the left and the right side pelvic fin base are posterior to the cleithrum in *Paralichthys*, *Ancylopsetta*, *Gastropsetta*, *Hippoglossina*, *Syacium*, *Cyclopsetta*, *Citharichthys*, and *Etropus*. In *Bothus* and *Chascanopsetta* the origin of the left side pelvic fin base is on the urohyal, which is well in advance of the cleithrum. The right side fin base of *Bothus* and *Chascanopsetta* is short, and its origin is well posterior to the cleithrum.

CAUDAL OSTEOLOGY

From late stage larvae to adults, the bothids show a correlation between caudal osteology and position of the pelvic fin bases (table 1). Species of *Paralichthys*, *Ancylopsetta*, *Gastropsetta*, and *Hippoglossina* have the dorsalmost principal caudal fin ray associated with an epural; the ventralmost principal caudal fin ray has a spur associated with it, and it is associated with the haemal spine of the penultimate vertebra. The count of principal caudal fin rays in this group, starting with the epural and ending with the haemal spine of the penultimate vertebra, is 1–2–6–4–3–1 or 1–2–6–5–2–1 in *Paralichthys*. In these genera neither of the plevic fin bases is on the median line and the origins of both pelvic fin bases are well behind the cleithrum.

Species of *Syacium*, *Cyclopsetta*, *Citharichthys*, and *Etropus* have all 17 principal caudal fin rays associated with the four hypural elements. The dorsal-to-ventral count of principal caudal fin rays on each hypural is 4–5–4–4. In these genera the left side pelvic fin base is on the median line, and its origin is well behind the cleithrum.

TABLE 1.—*Four generic groups which show a relation between the origins of the pelvic fin bases and number of principal caudal fin rays associated with caudal elements*

[Asterisks indicate the genera for which I have no identified larvae]

Genera	Pelvic fin (P^2)	Number of principal caudal fin rays associated with caudal elements
Paralichthys	Neither pelvic fin base on median line, both short-based; origins well behind cleithrum.	1–2–6–5–2–1
*Ancylopsetta**		1–2–6–4–3–1
*Gastropsetta**		
*Hippoglossina**		
Syacium	Ocular-side P^2 base on median line; origin posterior to cleithrum. Blind-side P^2 base above median line; origin posterior to cleithrum.	4–5–4–4
Cyclopsetta		
Citharichthys		
Etropus		
Engyophrys	Ocular-side P^2 base on median line; origin slightly anterior to or below cleithral tip. Blind-side P^2 base above median line; origin posterior to cleithrum.	1–3–5–4–3–1
*Trichopsetta**		
Monolene		
Bothus	Ocular-side P^2 base on median line, extending onto urohyal; origin anterior to cleithrum. Blind-side P^2 base above median line, short-based; origin posterior to cleithrum.	1–4–4–3–4–1
*Chascanopsetta**		

Species of *Engyophrys*, *Trichopsetta*, and *Monolene* have the dorsalmost and ventralmost principal caudal fin rays associated with the neural and haemal spines of the penultimate vertebra and have a count of 1–3–5–4–3–1. In these genera the left side pelvic fin base is on the median line and its origin is slightly anterior to the cleithral tip and to the origin of the right side base.

In *Bothus* and *Chascanopsetta* the count of principal caudal fin rays associated with the caudal elements is 1–4–4–3–4–1, starting at the neural spine and ending at the haemal spine of the penultimate vertebra. In *Bothus and Chascanopsetta* the left side pelvic fin base is on the median line and its origin is on the urohyal, on the right side the base is short, above the median line, and its origin is behind the cleithrum.

The number of principal caudal fin rays associated with caudal elements shows some variation, because a fin ray may be supported in part by two elements, such as hypurals, epurals, or neural or haemal spines.

DEVELOPMENT OF *CYCLOPSETTA FIMBRIATA* LARVAE

No information is available on the fertilized eggs or the yolk sac larvae of *C. fimbriata;* however, I do have certain observations on the larger larvae, including their identification, patterns of general growth, formation of fins, spination, pigmentation, migration of eyes, and sequence of ossification.

IDENTIFICATION OF LARVAE

Larvae of *C. fimbriata* are identifiable at very small sizes. The smallest larva in my sample (1.72 mm. SL) has a large head with a well-developed mouth. Hatching size is probably about 1.50 mm. SL or slightly smaller. Larvae of this species have two prominent transitory features (they may be generic) that are readily seen on the smallest larvae (fig. 3) : a small, single spine on the sphenotic region of the cranium and several small single spines on the preopercle (*Syacium* has larger sphenotic and preopercular spines). These spines persist throughout the larval stages (figs. 3–7) and are still evident during metamorphosis (that period when the eye is migrating). No fin rays are discernible in the finfold of the smallest larva (1.72 mm. SL). At about 2.10 mm. SL the first three elongate dorsal fin rays appear. Elongate dorsal fin rays (8–11 in the large larvae) persist throughout the larval stages (figs. 4–7). At about 3.00 to 3.30 mm. SL one to three elongate pelvic fin rays appear (fig. 4) and persist throughout the larval stages (figs. 4–7).

The right side eye is migrating in the largest larva in my sample (14.51 mm. SL). The dorsal edge of the migrating eye is above the middorsal ridge of the cranium. During metamorphosis the eye moves under the dorsal fin which is attached anteriorly to the ethmoid region of the cranium. The migrating eye had not yet begun to turn onto the left side, but it appeared about ready to move under the dorsal fin. Elongate dorsal and pelvic fin rays and head and preopercular spination persist (fig. 7).

Four transitory larval features help differentiate *C. fimbriata* and *Syacium* larvae from all other bothid larvae found along the southeastern coast of the United States: (1) a single spine in sphenotic region of the cranium, (2) several single preopercular spines, (3) relatively high numbers of elongate anterior dorsal fin rays, and (4) three elongate pelvic fin rays (figs. 3–7). Compared to *Cyclopsetta*, *Syacium* has larger and heavier spines, fewer elongate dorsal fin rays, and relatively shorter elongate pelvic fin rays. The sphenotic spine is surrounded by concentric rings on large *Cyclopsetta* larvae but by a crenulated cap on *Syacium* larvae. The origins of the pelvic fin bases in relation to each other and to the cleithrum and the transitory larval characters provide the generic identity of *Cyclopsetta* larvae.

Three species of *Cyclopsetta* occur in the western North Atlantic Ocean (Gutherz, 1967). *C. fimbriata* is the only species known from the Atlantic coast of the United States, *C. decusata* is known only from the type, and *C. chittendeni* is found along the coast of the United States only in the Gulf of Mexico. The distribution of these species excludes all known species of *Cyclopsetta* except *fimbriata* from consideration for my larvae.

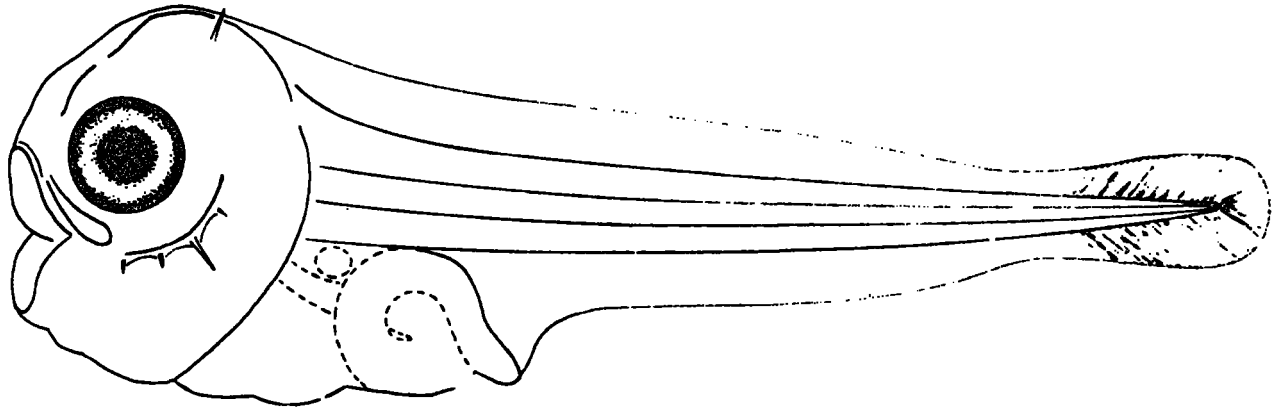

FIGURE 3.—Larva of *Cyclopsetta fimbriata*, 1.89 mm. SL. Note sphenotic and preopercular spination. Pectoral fin is omitted to show swim bladder and gut.

GENERAL GROWTH PATTERNS

Head length and body depth show a uniform rate of increase with standard length throughout the size range of my sample (figs. 8–9).

Upper jaw length shows a uniform rate of increase with standard length in larvae longer than about 4 mm. SL, but smaller larvae have a faster rate of increase (fig. 10).

Lower jaw length increases at a uniform rate with standard length in larvae between about 4 and 13 mm. SL; but larvae smaller than about 4 mm. SL and longer than 13 mm. SL have a faster rate of increase (fig. 11).

Snout length increases only slightly in specimens up to about 2.7 mm. SL; between about 2.7 and 4 mm. SL snout length increases at its fastest rate; and larvae larger than about 4 mm. SL have a uniform but slower rate of increase with standard length (fig. 12).

Eye diameter increases at a uniform rate with standard length in larvae longer than about 3.5 mm. SL; the rate is faster in smaller larvae (fig. 13). Eye diameter as a percentage of head length decreases throughout the size range in my sample (fig. 14); the fastest decrease is between head lengths of about 0.5 and 1.5 mm. (1.8 to about 4 mm. SL).

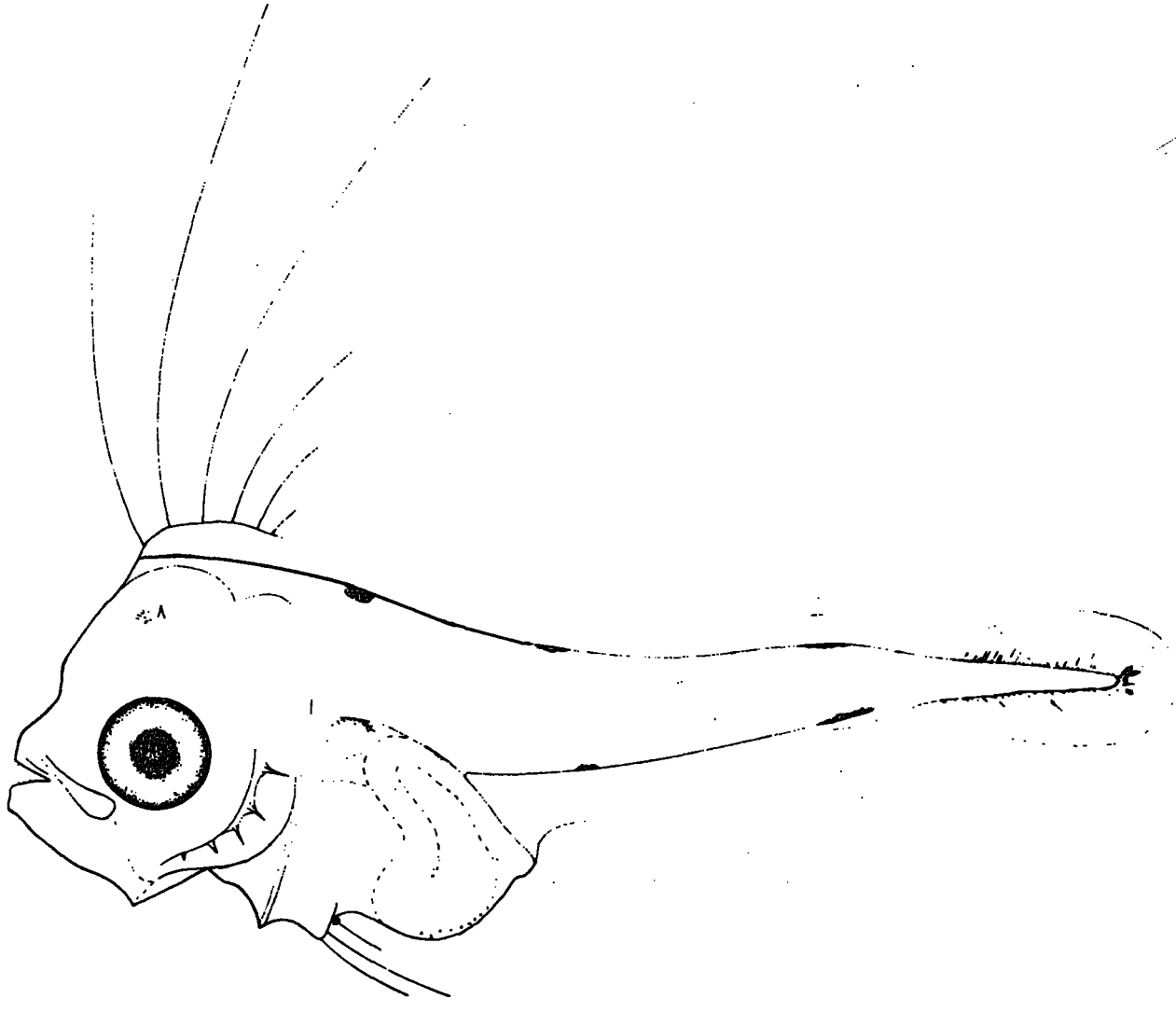

FIGURE 4.—Larva of *Cyclopsetta fimbriata*, about 3.0 mm. SL. Note sphenotic and preopercular spination, elongate dorsal and pelvic fin rays, and pigmentation. Pectoral fin is omitted to show swim bladder, gut, and pigmentation on dorsal portion of swim bladder and gut.

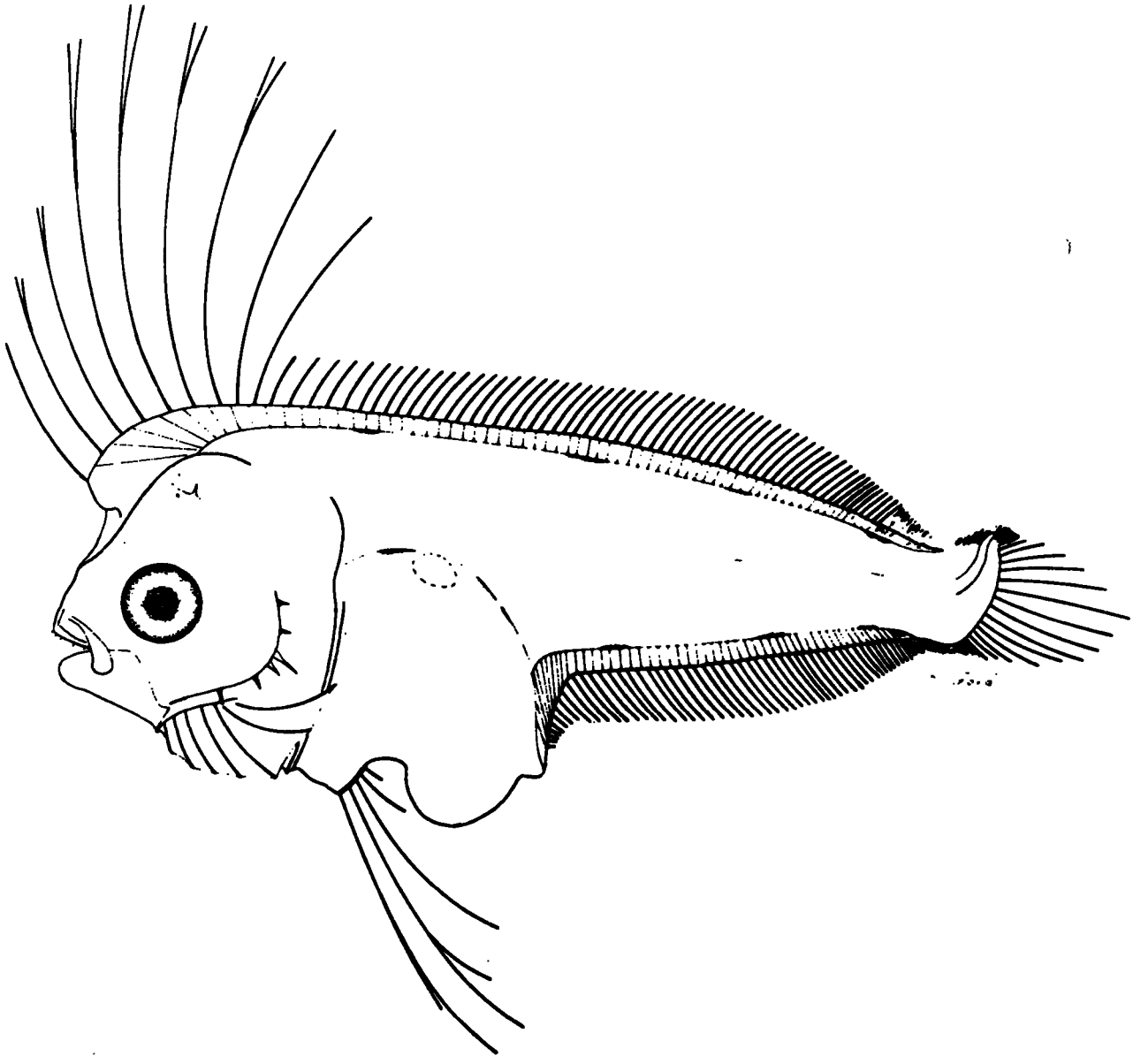

FIGURE 5.—Larva of *Cyclopsetta fimbriata*, 6.9 mm. SL. Note sphenotic and preopercular spination, elongate dorsal and pelvic fin rays, and pigmentation. Pectoral fin is omitted.

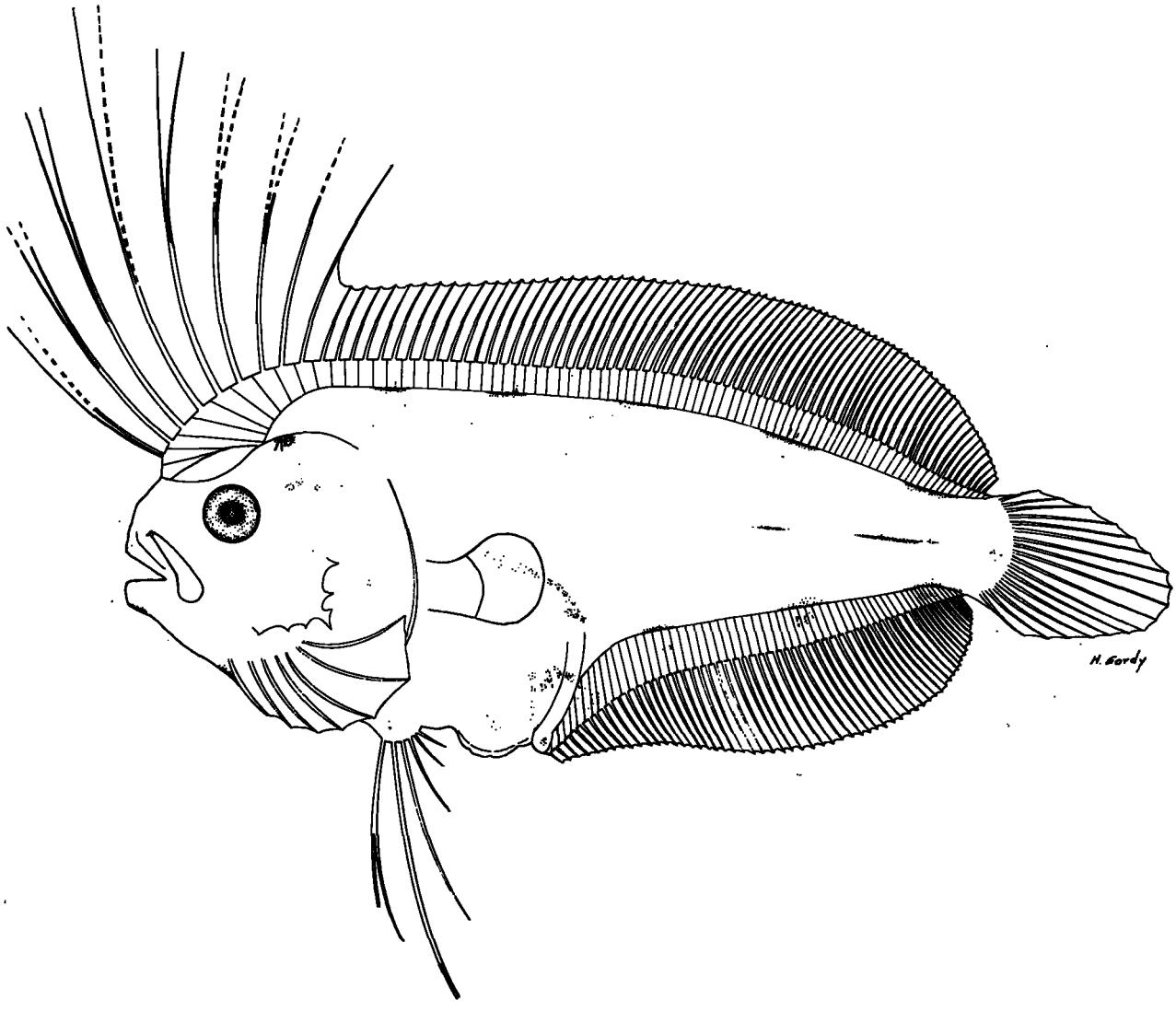

FIGURE 6.—Larva of *Cyclopsetta fimbriata*, 12.9 mm. SL. Note sphenotic and preopercular spination, elongate dorsal and pelvic fin rays, pigmentation, and area under anterior portion of the dorsal fin through which the right side eye will migrate.

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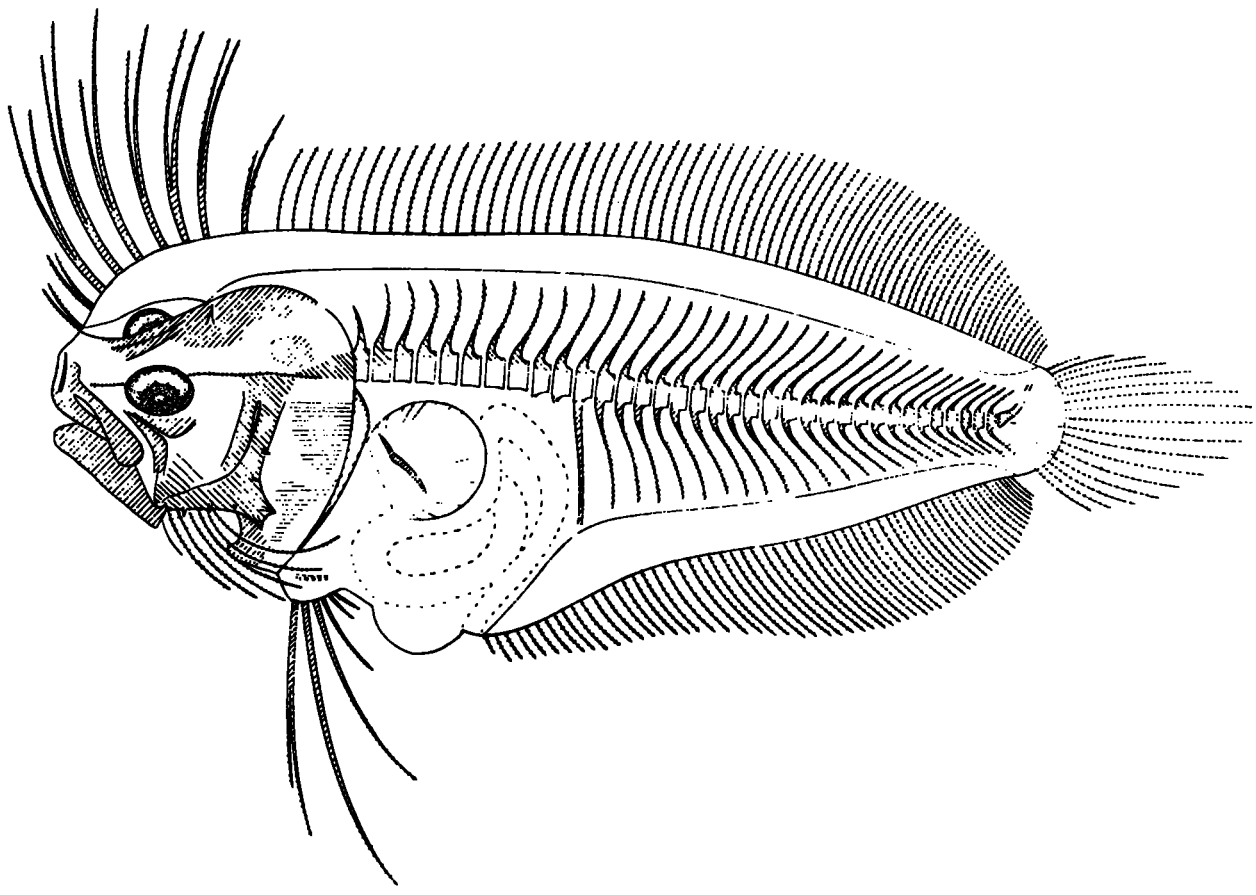

FIGURE 7.—Larva of *Cyclopsetta fimbriata*, 14.0 mm. SL. Larva has been cleared and stained, and all bone that has absorbed alizarin red S is shaded. Note sphenotic and preopercular spination, elongate dorsal and pelvic fin rays, right side eye under anterior part of dorsal fin will migrate through head. Ossification is not yet complete.

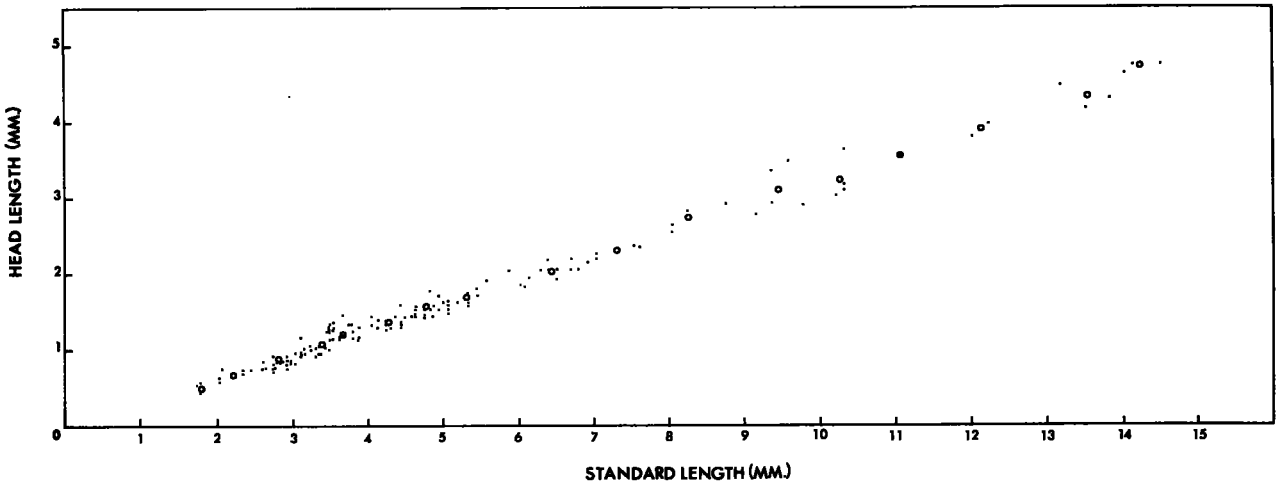

FIGURE 8.—Relation of head length to standard length of *Cyclopsetta fimbriata* larvae. Dots represent individual specimens, and open circles represent means (see app. tables 1 and 2).

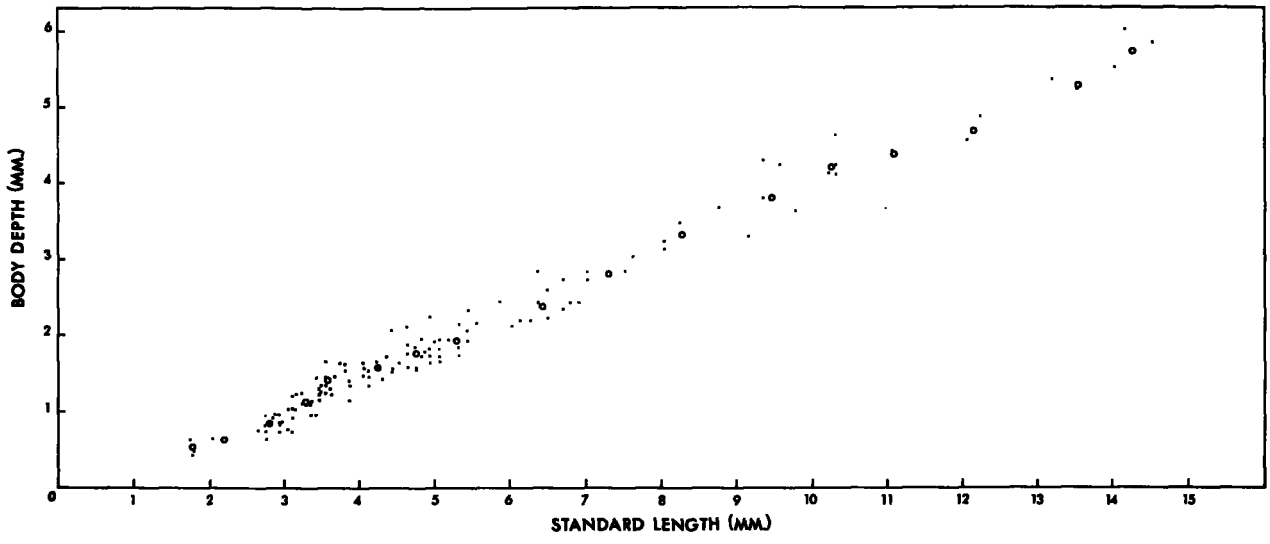

FIGURE 9.—Relation of body depth to standard length of *Cyclopsetta fimbriata* larvae. Dots represent individual specimens, and open circles represent means (see app. tables 1 and 2).

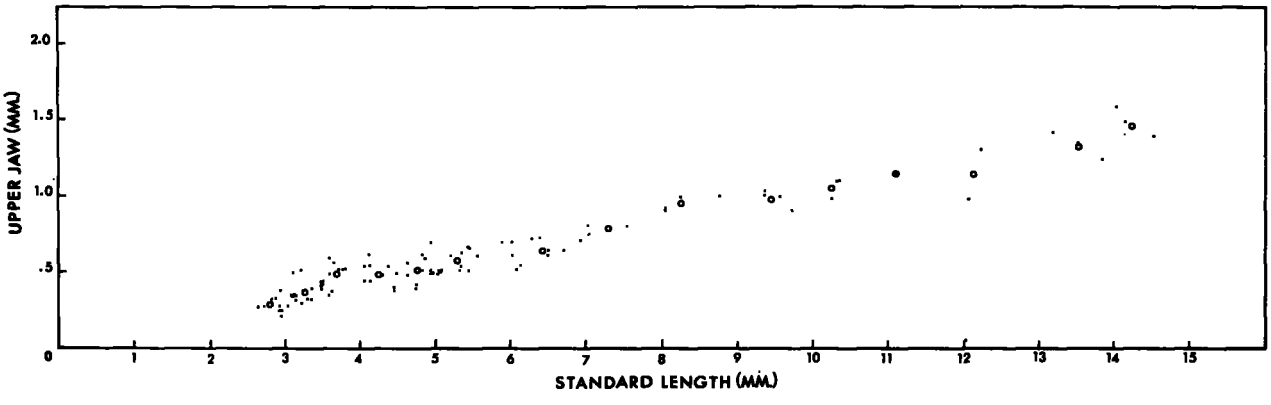

FIGURE 10.—Relation of upper jaw length to standard length of *Cyclopsetta fimbriata* larvae. Dots represent individual specimens, and open circles represent means (see app. tables 1 and 2).

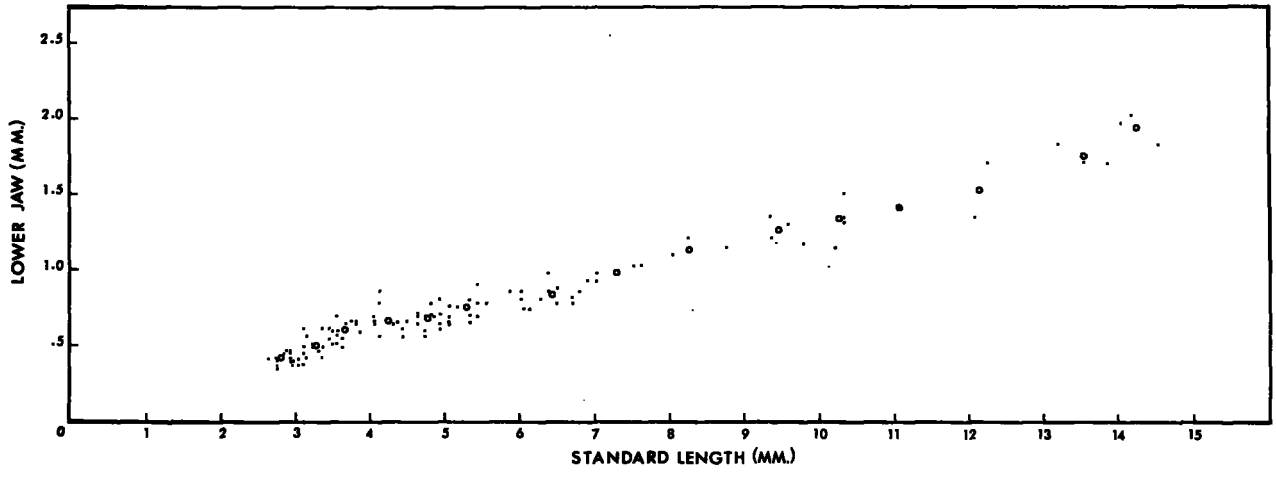

FIGURE 11.—Relation of lower jaw length to standard length of *Cyclopsetta fimbriata* larvae. Dots represent individual specimens, and open circles represent means (see app. tables 1 and 2).

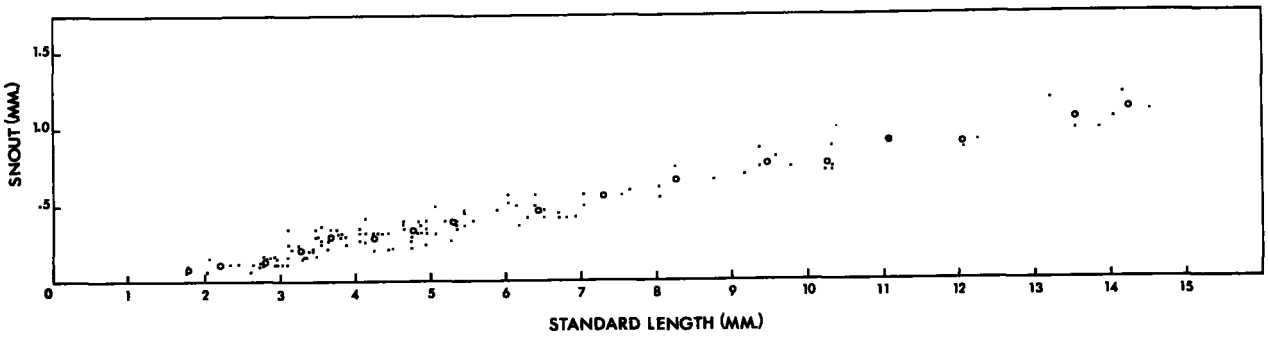

FIGURE 12.—Relation of snout length to standard length of *Cyclopsetta fimbriata* larvae. Dots represent individual specimens, and open circles represent means (see app. tables 1 and 2).

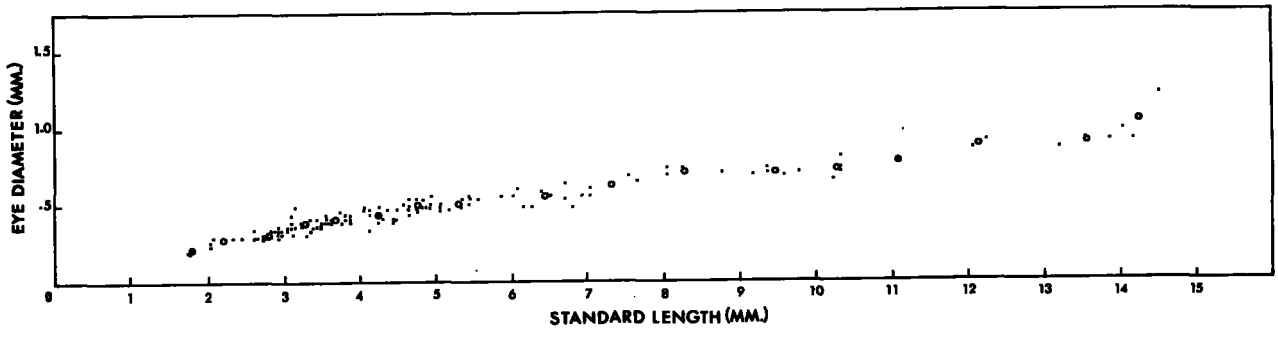

FIGURE 13.—Relation of eye diameter to standard length of *Cyclopsetta fimbriata* larvae. Dots represent individual specimens, and open circles represent means (see app. tables 1 and 2).

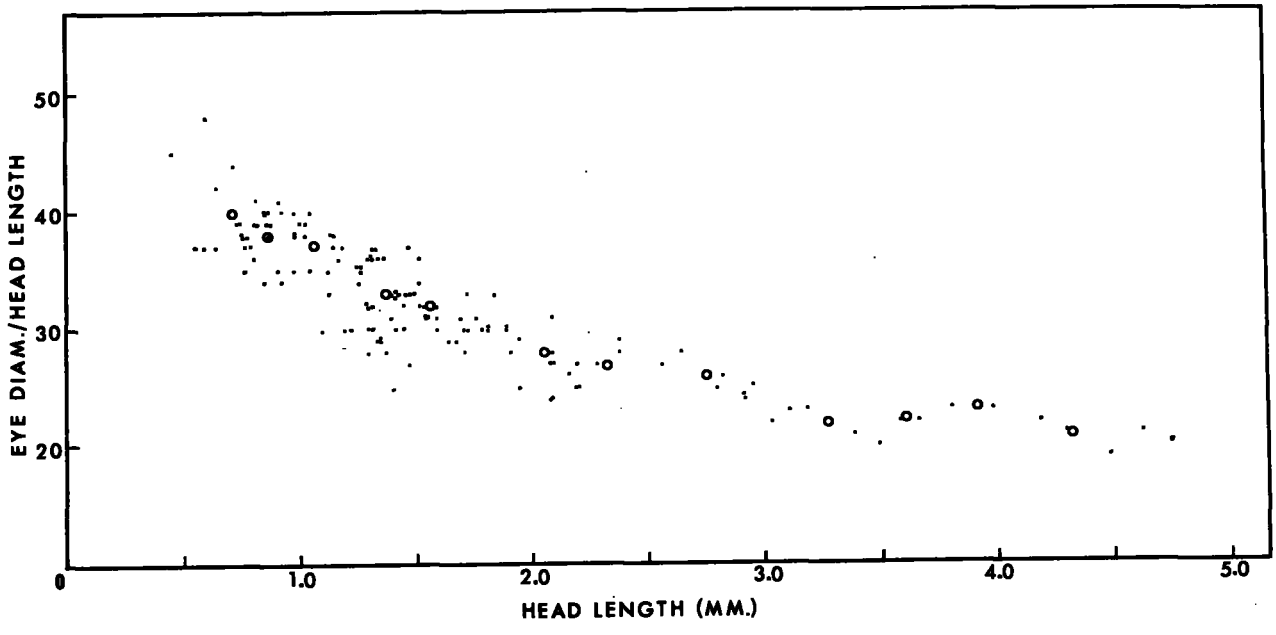

FIGURE 14.—Decrease in eye diameter relative to head length of *Cyclopsetta fimbriata* larvae. Dots represent eye diameter as percentage of head length of individual specimens, and open circles represent means (see app. tables 1 and 2).

Gill rakers begin to develop as elevations on the dorsal surface of the ceratobranchial. They are first seen when the larvae are about 8 mm. SL. Four or five lower-limb gill rakers are first seen on larvae about 9 mm. SL. They are short, blunt, well separated, and located on the ceratobranchial. By 10.0 mm. SL the number of lower-limb gill rakers has increased to seven and they are found on the ceratobranchials and hypobranchials. The adult complement of 8 to 10 gill rakers on the lower limb is reached at about 13.5 mm. SL. Gill rakers are first seen on the epibranchial in 13.5 mm. SL larvae, which have a single gill raker located immediately above the angle.

FIN FORMATION

In the development of *C. fimbriata* the pectoral fin is the first to appear and the last to complete its development. The caudal fin completes development first, followed in order by the dorsal, anal, and pelvic fins. By about 8 mm. SL the adult complement of fin rays is present in the caudal, dorsal, and anal fins (fig. 2).

Pectoral Fin

The pectoral fin is present on my smallest larva (1.72 mm. SL) and is not fully developed on my largest specimen (14.5 mm. SL). Initially it is large and rayless.

Caudal Fin

The fully formed caudal fin has 17 principal fin rays associated with the four hypural elements. The dorsal and ventralmost caudal fin rays are simple; the remaining rays are branched. Principal caudal fin rays are separable into two groups. The nine upper rays are associated with the two superior hypurals and the eight lower rays with the two inferior hypurals (4–5–4–4). No caudal fin rays are associated with neural and haemal spines of the penultimate vertebra. A ventral thickening near the posterior end of the notochord is seen on specimens about 3.5 mm. SL. This thickened tissue develops into the two median hypural plates and their associated caudal fin rays. The first four caudal fin rays to develop are seen first on a 5.44 mm. SL specimen and appear simultaneously (fig. 2). They develop at an oblique angle to the notochord and are divided into two groups, upper and lower. This division separates the caudal fin into superior and inferior components. By about 8 mm. SL the notochord has turned dorsally, the hypurals and caudal fin rays are arranged parallel to the axis of the body, and all principal caudal fin rays are developed (fig. 2), but the caudal osteology is not fully developed until a larger size.

Dorsal Fin

Dorsal fin ray development is an important taxonomic character in larval flatfish. These fin rays begin to develop in a thickened area above the nape on specimens of about 2 mm. SL. My smallest specimen with dorsal fin rays (three elongate rays) is 2.08 mm. SL (see app. table 1). The origin of the dorsal fin base moves anteriorly on the larvae until the fin base is over the eye; at this time dorsal fin rays begin developing posterior to the nape. All elongate dorsal fin rays develop first. The origin of the dorsal fin continues to shift anteriorly until it becomes attached to the ethmoid region of the cranium ahead of the eye. The first three fin rays must develop simultaneously; all but three of the specimens between 2 and 3 mm. SL have three or four fin rays (one with two, and two with five). The number of fin rays on all but four specimens between 3 and 5 mm. SL does not exceed 10 (one with 11 and three with 14), and most of the rays are elongate. The number of fin rays increases rapidly between 5 and 8 mm. SL; at 8 mm. SL the adult complement of 78 to 87 fin rays is present (fig. 2). Three of my 19 larval specimens exceeding 8 mm. SL had 77 fin rays, and one had 76.

Anal Fin

Fifteen anal fin rays were present on a 5.9 mm. SL specimen; none were discernible on smaller specimens (fig. 2; app. table 1). The number of fin rays increased rapidly, as in the dorsal fin, and the adult complement of 59 to 67 fin rays was developed by about 8 mm. SL (fig. 2). Four of 19 specimens exceeding 8 mm. SL had fin ray counts of 58, three had fewer than 58, and the others had counts between 59 and 67 (see app. table 1).

Pelvic Fins

Pelvic fin bases develop early. The left-side fin base and its three elongate anterior fin rays develop earlier than the right-side fin base. The left-side fin base is first noted on specimens of about

2.5 mm. SL as a thickening on the ventral edge of the body immediately anterior to the gut, but the right-side base does not appear until about 3.5 mm. SL. My smallest specimen with pelvic fin rays (left side, and elongate rays) was 3.0 mm. SL. The first right-side fin ray is seen on a 5.3 mm. SL specimen. The three elongate pelvic fin rays on the left side develop simultaneously. They are present on all specimens but two (one with a single fin ray and one with two fin rays). The fourth left fin ray develops at about 5 mm. SL, and the fifth and sixth rays by about 10 mm. SL. Each fully developed pelvic fin has six fin rays. The three elongate fin rays of the left side are thickened and heavier than the other pelvic fin rays and extend posteriorly to about the caudal peduncle; they are often broken. None of the other pelvic fin rays is elongate. The origins of the pelvic fin base are equidistant behind the cleithrum.

LARVAL SPINATION

A single sphenotic spine and a series of preopercular spines (figs. 3–7) persist throughout the size series of my larval specimens (1.72–14.51 mm. SL). These spines are smaller but similar in position and shape to those reported for *Syacium* by Kyle (1913) and Aboussouan (1968). The sphenotic spine becomes relatively smaller as the larvae grow. The spine is surrounded by concentric rings that are first noted on specimens of about 4.6 mm. SL. Four to six small sharp spines are present on the preopercular margin; two or three of these are on the ventral edge, a larger single spine is at the angle, and two more small spines are on the posterior edge. The large spine at the angle of the preopercle thickens, and a spur develops on the upper posterior edge of the spine on larger larvae. These spines do not alter position or shape but become relatively smaller with increasing size of the larvae. The sphenotic and preopercular spines can be traced through the developmental series and are important in identifying this group of larvae (figs. 3–7).

PIGMENTATION

Pigment on all of the *Theodore N. Gill* material is faded, but pigment patterns are readily seen on the fresh *Oregon* material. In my sample, pigment is first seen on a 2.8 mm. SL specimen—a large melanophore over the base of each sphenotic spine, and another melanophore on the gular region between the posterior end of the lower jaws and the tip of the cleithrum. The dorsal portion of the swim bladder and the dorsal loop of the gut are heavily pigmented. On a 3.2 mm. SL specimen the melanophores at the bases of the sphenotic spines have faded, but those on the gular region and along the dorsal aspect of the gut remain. Three clusters of melanophores are present on the dorsal edge, and two are on the ventral edge of the body. The anteriormost is on the dorsal edge of the body over the pectoral fin base (there is no corresponding ventral cluster of melanophores). The other two dorsal clusters of melanophores have corresponding ventral clusters. The middle spots are immediately behind the gut region, at about the midpoint of the body (TL), and the posterior spots are slightly anterior to the caudal peduncle (fig. 4). A series of small melanophores can be seen on the ventral edge of the gut between the vent and the anterior portion of the gut cavity. Pigmentation is essentially the same on specimens up to about 4 mm. SL, but the number of melanophores increases. Specimens between 4 and 5 mm. SL have a large melanophore on each opercle behind the eye and another on the median line at the origin of the pelvic fin base. The dorsal portion of the gut has two areas of dark pigment; the anteriormost is on the upper half of the swim bladder and the other is above the loop of the intestine.

At about 5 mm. SL the melanophore on the gular region has disappeared, but additional clusters of melanophores have appeared, one dorsal and one ventral, between the middle and posteriormost cluster but nearer the posteriormost cluster. The two new clusters are of equal size and are smaller than those nearest to them. The remaining pigment is similar to that seen on the smaller larvae. Shortly after appearance of the third ventral pigment cluster the posteriormost ventral cluster increases in length and becomes longer than its corresponding dorsal area.

By 7 mm. SL a fifth dorsal cluster has appeared between the first two clusters. Two pigment clusters have developed along the lateral septum, corresponding in position with the two posterior dorsal and ventral clusters. Pigment is present over the entire swim bladder on the left side and absent on the right side. Pigmentation remains essentially the same through the rest of the larval

series in my sample, except for darkening and the appearance of pigment at the distal edge of the caudal peduncle, in the branchial chambers, and around the urohyal (figs. 5 and 6).

MIGRATION OF THE EYE

Specimens of 7 mm. SL are symmetrical; the right eye has not begun to migrate (fig. 5). The dorsal fin continues its development anteriorly, and its origin is over the anterior edge of the eye. The supraorbital bars on the cranium have not begun to become modified.

By about 8 mm. SL the right eye has moved only slightly; the origin of the dorsal is above and posterior to the ethmoid region of the cranium and the origin of the fin base remains unattached. Tissue between the ventral edge of the anterior portion of the dorsal fin and the frontal region of the cranium is becoming thin, and the supraorbital bars have begun to shift onto the ocular sides as an accompanying depression begins to form above the left eye.

By 10.5 mm. SL the right eye has migrated dorsoanteriorly but its upper edge is not yet level with the supraorbital bars; the origin of the dorsal is attached to the ethmoid region of the cranium and its point of attachment has shifted onto the right side of the head, over the nostrils. The right side is the blind side in the adult. The area of thin tissue between the dorsal fin and the supraorbital bars is wider. The supraorbital bars continue their shift to the left side, and the depression of the cranium above the left eye is larger.

On a 14 mm. SL specimen the upper edge of the right side eye is visible through the thin tissue below the dorsal fin (fig. 7). The shifting of the supraorbital bars has created a large depression over the left eye. The origin of the dorsal fin remains attached. The right eye has not yet begun to move through the head onto the left side. In larger specimens the eye will move through the head in the area between the dorsal fin and the depression created by the shift of the supraorbital bars.

SEQUENCE OF OSSIFICATION

I cleared and stained several specimens to determine the sequence of ossification. The degree of ossification can be assessed by the intensity of the stain (alizarin red S) absorbed by the bone. In this discussion I consider any bone that absorbed stain to be ossified.

On a 1.7 mm. SL specimen only the cleithrum, the distal edges of the preopercle and preopercular spines, and the sphenotic spine and its base showed any ossification.

By 3 mm. SL some ossification is seen in the cranial cap, lower jaw, premaxillary, and the four elongate dorsal fin rays. By 3.5 mm. SL the three elongate pelvic fin rays, the maxillary, four branchiostegal rays, and six elongate dorsal fin rays are ossified. The palatine and parasphenoid are stained and extend from the symphysis of the upper jaw to the cleithrum; these bones will form part of the floor of the neurocranium. At this size all stained areas are in the head and pelvic fin region. Six canine teeth are present in the lower and four in the upper jaw, but none are stained. A slight thickening on the ventral edge of the posterior part of the notochord is the rudimentary hypural, and it is only slightly ossified, if at all.

Ossification is still restricted to the head and pelvic fin base region at 4.1 mm. SL. All seven branchiostegal rays, the urohyal, and the preopercle and opercle in the opercular series are now ossified. The vertebrae and neural and haemal spines have not begun to ossify. Ossification at 4.9 mm. SL is essentially similar to that of the 4.1 mm. SL specimen; again the anterior neural and haemal spines are visible but are not stained. They are not attached to the vertebrae and appear as thin lines between the vertebrae and the dorsal and anal fin rays.

At 5.5 mm. SL the right pelvic fin base, three or four caudal fin rays (but not the hypural elements), the dorsal aspect of the subopercle, and some vertebrae and associated neural and haemal spines have begun to ossify. The 16 anterior neural spines and the anterior seven haemal spines, and the dorsal rim and sides of the neural arch on the second, third, and fourth vertebrae are lightly stained. The first vertebra and its neural spine are not stained. The occipital region of the neurocranium and the scapula have begun to ossify.

The areas of ossification, as determined by absorption of alizarin red S stain, are larger and the color is more intense at 6.4 mm. SL than on smaller specimens. At this size the notochord is upturned and two hypural elements are differentiated. Ten caudal fin rays are stained, and five are associated

with each hypural element. The notochord has neural and haemal spines on nearly its full length. Most neural arches, but only the anterior haemal arches, are stained. Pterygiophores of the anterior elongate dorsal fin rays are developing. About 40 dorsal and 24 anal fin rays are stained. The interopercle has begun to ossify, and all four opercular elements show some ossification. The supraorbital bars are stained and are visible as anterior extensions of the neurocranium. The auditory region of the neurocranium is partially stained, and the post cleithrum is ossifying.

By 10 mm. SL ossification has progressed considerably, and many bones in the head, vertebrae, and caudal fin can be recognized. At about 10 mm. SL ossification is noted in the hypural elements, the basal part of the urostyle, and the parapophysis of the last abdominal (precaudal) vertebra. The dorsal aspects of the posterior 14 and the anteriormost 3 or 4 vertebrae are lightly stained; the remaining vertebrae are not stained. All neural and haemal spines and arches are ossified except for those on the penultimate vertebra. There are 16 caudal fin rays: Four are associated with each of the two inferior hypurals, the superior hypurals are indistinguishable. Four to six pelvic fin rays have developed on each fin base, and the pelvic bone is beginning to ossify. The supraorbital bars extend forward; their anterior edge is above the nostril. The entopterygoid, which is immediately above the pterygoid, is lightly stained. Bones of the lower jaw suspension can be identified; the quadrate, hyomandibular, and pterygoid are lightly stained. The supracleithrum and posttemporal region of the cranium can be distinguished. The upper jaw now has about 10 teeth and the lower 16; those near the symphysis are relatively small and close together. A "cartilaginous" bar extends posteriorly along the ventral median edge of the gut from the distal edge of the pelvic fin base to below the liver. The anterior ventral edge of the urohyal is hooked and pointed forward.

Ossification has changed little at about 14 mm. SL except on the vertebrae (fig. 7). The first abdominal (precaudal) vertebra is completely ossified, and the dorsal aspect and one-third to one-fourth of the lateral surfaces of the other abdominal vertebrae are ossified. The parapophyses of the last four abdominal vertebrae are also ossified, but no ribs are seen. Ossification of the parapophyses begins with the last abdominal vertebra and proceeds anteriorly to the fifth vertebra, the last one with a parapophyses. The first through the 18th caudal vertebrae show the same degree of ossification; posteriorly they become progressively more ossified until ossification is complete on the last four vertebrae. Interneurals and interhaemals are developing between the fifth and 10th neural and haemal spines. The enlarged pterygiophore, which is associated with the first 10 to 12 anal fin rays, is now lightly stained.

My largest larva (14.5 mm. SL) is stained and shows essentially the same degree of ossification as the 14 mm. SL specimen. The vertebral column, pterygiophores of the dorsal and anal fins, and all bones of the neurocranium and branchiocranium are not completely ossified. The supraorbital bars extend forward onto the ethmoid region and form the frontals. The right side supraorbital bar appears to be partially reabsorbed as suggested by its upturned anterior medial edge in the sphenotic region and its position and thinness. The left supraorbital bar has moved closer to the left eye. After movement of the supraorbital bar is complete the left side bar and part of the right side bar form the interorbital bar, and the remaining part of the right supraorbital bar is reabsorbed. At a larger size the right eye will move under the dorsal fin and stop at the interorbital bar. The sphenotic and preopercular spines are still present at 14.5 mm. SL but will eventually be reabsorbed or broken off and leave the surface smooth.

SPAWNING AND DISTRIBUTION

Larvae were collected between Jupiter Inlet, Fla., and Cape Hatteras, N.C. (fig. 1) in surface waters over depths of 11 to 2,510 m. (6–1,372 fath.); 21 stations were in depths greater than 183 m. (100 fath.) and 54 stations in depths less than 183 m.

Specimens were collected primarily north of lat. 30° N. (70 collecting sites were north and only 5 were south of lat. 30° N.). Sixty-nine larvae were taken at 35 stations occupied at night, and 102 were taken at 38 stations occupied during the day. No larvae were collected between November and April; one larva was taken in April and one in November; and the rest in May to October (fig. 15).

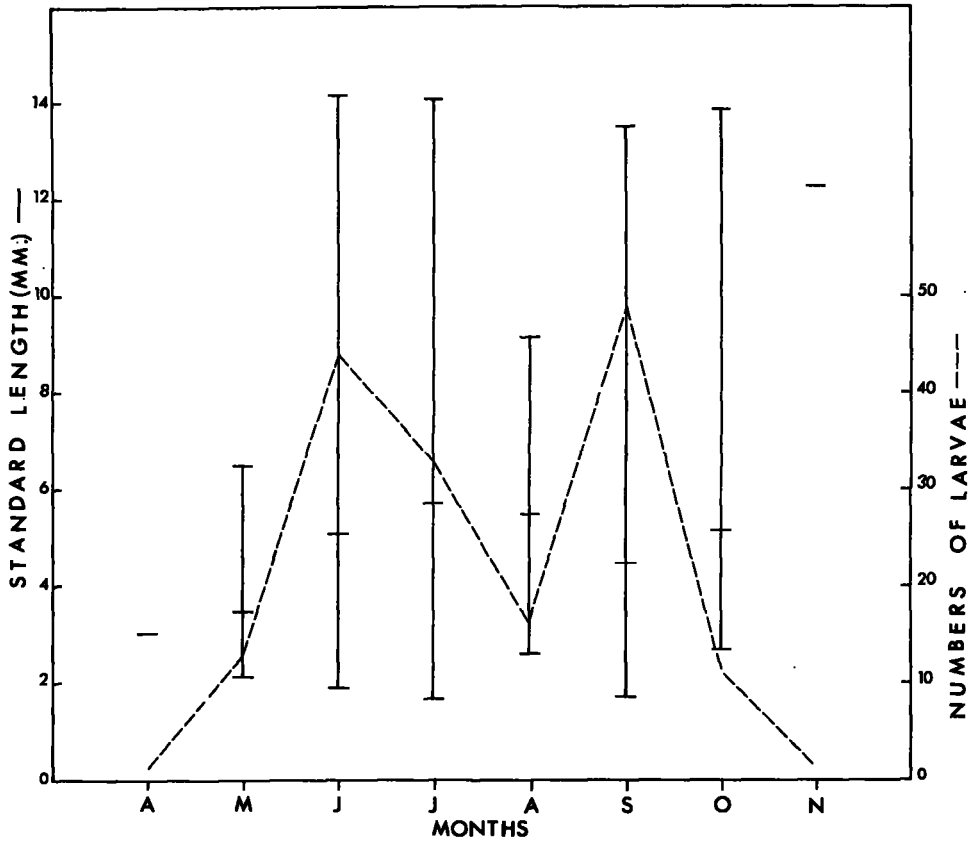

FIGURE 15.—Size range and mean size of larvae collected from April to November. Frequency of larvae per month also shown.

The *Theodore N. Gill* data by themselves show a single spawning peak in September, but the combined *Theodore N. Gill* and *Oregon* data suggest a bimodal spawning period with peaks in June and September. The first larvae appear in April, and numbers increase sharply until June; after September the numbers decrease sharply to November. Larvae 2.6 mm. SL and smaller were collected each month from May through October. I estimate that hatching size is about 1.5 mm. SL; therefore, spawning must occur throughout this period. The mean size of the larvae increases through July and then decreases in September. This size decrease is correlated with a spawning peak (fig. 15). My samples contain no larvae exceeding 9 mm. SL until the last week in June, but larvae of this size are present in succeeding months through November (fig. 15). These size data support the supposition that spawning begins in the spring.

I have not seen spawning fish, but I have examined gonads from *C. fimbriata* taken throughout the year off Cape Kennedy, Fla. None of the gonads were ripe, but the ovaries enlarged progressively from spring to fall. In the winter the ovaries are very thin and flat. My examination of gonad development indicates a spawning period from early spring to late fall—again supporting conclusions based on the samples of larvae.

I tried to determine where *C. fimbriata* spawns by analyzing the collection data for 28 smaller larvae (1.7 mm.–3.0 mm. SL). These specimens were collected at 17 stations on *Theodore N. Gill* and *Oregon* cruises. Ten of the 17 stations were occupied during daylight; of these six were in 46 m. (25 fath.) or less. Three of the seven nighttime stations were in depths of 46 m. (25 fath.) or less. Small larvae were collected from May through October from Florida to North Carolina. Because hatching size is estimated to be about 1.5 mm. SL, specimens less than about 2.0 mm. SL must have

been collected close to the spawning area, but this view may be erroneous because the time required for hatching of the eggs is unknown. Six specimens (1.72–2.01 mm. SL) were collected from five stations, at the surface in 22 to 450 m. (12–246 fath.) during both day and night. These small larvae were caught from July to September from Georgia to North Carolina. It appears that *C. fimbriata* spawns from April to October throughout the entire collection area on the Continental Shelf and that most spawning is in waters of 46 m. (25 fath.) or less. Delineation of the spawning area of *C. fimbriata* must await the collection or observation of spawning fish.

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Elbert H. Ahlstrom of the BCF Fishery-Oceanography Center, La Jolla, Calif., reviewed the manuscript and made many helpful suggestions. Assistance by various staff members of the laboratory included review of the manuscript, preparation of figures 3 through 7, and preparation of stained material.

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APPENDIX

TABLE 1.—*Selected measurements and counts of larval* Cyclopsetta fimbriata

Measurements													Counts	
Standard length	Head length (HL)		Body depth (BD)		Eye diameter (ED)		Upper jaw length (UJL)		Lower jaw length (LJL)		Snout length (SN)		Pelvic fin origin to tip of cleithrum [1] *blind-side* ocular-side	Dorsal fin rays	Anal fin rays
Mm.	*Mm.*	*HL/SL*	*Mm.*	*BD/SL*	*Mm.*	*ED/HL*	*Mm.*	*UJL/HL*	*Mm.*	*LJL/HL*	*Mm.*	*SN/HL*	*Percent*	*Number*	*Number*
1.72	0.54	32			0.20	37									
1.76			0.42	24	.20	45					0.07	16			
1.79	.59	33	.49	27	.22	37					.10	17			
1.89															
2.01	.64	32	.64	32	.24	37					.07	11			
2.01	.59	29			.27	48									
2.08	.76	37			.29	38					.15	20		3	
2.33	.69	30			.29	42					.12	17		4	
2.33	.74	32			.29	39					.12	16		4	
2.45	.74	30			.29	39					.12	16		4	
2.60	.86	33			.34	40								4	
2.60	.76	29			.29	38					.07	9		3	
2.64	.78	30	.76	29	.29	37	0.27	35	0.42	54	.12	15		3	
2.72	.81	30	.81	30	.29	36	.27	33	.39	48	.12	15		3	
2.72	.78	29	.81	30	.27	35			.34	44	.10	13		3	
2.72	.73	27	.73	27	.32	44			.37	51				4	
2.72	.93	34	.96	35					.42	45				3	
2.75	.76	28	.64	23	.29	38					.10	13		2	
2.79	.86	31	.86	31	.29	34					.17	20		4	
2.83	.86	30	.91	32	.34	40	.32	37	.44	51	.15	17		3	
2.87	.88	31	.98	34	.34	39	.32	36	.47	53	.15	17	83	5	
2.91														4	
2.91	.83	29	.86	30	.32	39	.27	33	.39	47	.17	21		3	
2.91	.78	27	.71	24	.29	37	.24	31	.42	54	.12	15		3	
2.91	.93	32	.98	34	.37	40			.47	51	.17	18	120	5	
2.91	.88	30	.83	29	.34	39	.37	42	.44	50	.12	14	85	3	
2.95	.86	29	.86	29	.34	40			.37	43	.15	17	83	4	
2.95	.83	28			.32	39	.24	29	.39	47	.12	14		3	
3.03	.83	27	.78	26	.34	41	.27	33	.37	45	.12	14		3	
3.03	.98	32	1.03	34	.37	38			.42	43	.12	12		4	
3.10														4	
3.10					.44	37	.49	42	.61	52	.34	29		6	
3.10	.93	30			.32	34	.34	37	.44	47	.24	26	100	4	
3.10	.91	29	.91	29	.37	41			.37	41	.12	13	100	4	
3.10	.98	32	1.03	33	.39	40	.34	35	.49	50	.17	17	100		
3.14	1.03	34	1.23	39	.49	48	.34	33	.56	54	.22	21		7	
3.14	.98	31	1.03	33	.37	38	.32	33	.42	43	.22	22		5	
3.22	1.00	31	1.25	39	.39	39			.51	51	.24	24		5	
3.22	1.05	33	1.10	34	.37	35	.29	28	.49	47				5	
3.30	.91	28			.32	35	.32	35	.47	52	.20	22		4	
3.30	1.03	31	1.10	33	.39	38					.15	15	100	5	

See footnote at end of table.

TABLE 1.—*Selected measurements and counts of larval* Cyclopsetta fimbriata—Continued

Measurements													Counts	
Standard length	Head length (HL)		Body depth (BD)		Eye diameter (ED)		Upper jaw length (UJL)		Lower jaw length (LJL)		Snout length (SN)		Pelvic fin origin to tip of cleithrum [1] *blind-side* ocular-side	Dorsal fin rays	Anal fin rays
Mm.	*Mm.*	*HL/SL*	*Mm.*	*BD/SL*	*Mm.*	*ED/HL*	*Mm.*	*UJL/HL*	*Mm.*	*LJL/HL*	*Mm.*	*SN/HL*	*Percent*	*Number*	*Number*
3.34	1.05	31	1.10	33	0.42	40	0.39	37	0.61	58	0.17	16	100	5	
3.35	.98	29	.98	29	.34	35	.32	33	.42	43	.17	17		4	
3.38	.98	29	1.13	33	.37	38			.49	50	.20	20	71	6	
3.41	1.03	30	.98	29	.37	36					.20	19	88	5	
3.42	1.25	37	1.45	42	.42	34			.61	49	.22	18		6	
3.48	1.22	35	1.30	37	.37	30	.42	34	.54	44	.34	28	100	6	
3.48	1.27	37	1.22	35									71	6	
3.48	1.30	37	1.30	37	.37	28	.44	34	.54	42	.29	22	75	8	
3.48	1.00	29	1.15	33									88	4	
3.49	1.36	39	1.35	39	.39	29	.39	29	.51	37	.29	21	125	7	
3.49	1.13	32	1.27	36	.37	33	.42	37	.54	48			83	6	
3.54	1.37	39	1.67	47	.39	28	.59	43	.69	50	.37	27	83	7	
3.54	1.30	37	1.35	38	.39	30	.49	38	.56	43	.27	21		7	
3.54	1.15	33	1.25	35	.42	37	.34	30	.51	44	.24	21	80	9	
3.54	1.27	36	1.47	42	.44	35	.49	39	.59	46	.27	21		7	
3.61	1.18	33	1.30	36	.42	36	.37	31	.54	46	.27	23		6	
3.61	1.13	31	1.22	34	.39	35			.49	43	.22	19	88	4	
3.67	1.20	33												6	
3.67	1.47	40	1.47	40	.39	27	.56	38	.64	44	.34	23	77	8	
3.73	1.32	35	1.64	44	.47	36	.51	39	.66	50	.34	26		5	
3.76	1.32	35			.39	30					.32	24		7	
3.80	1.15	30	1.54	41	.44	38	.51	44	.66	57	.29	25		7	
3.80	1.25	33	1.62	43	.42	34	.51	41	.64	51	.32	26		7	
3.88	1.15	30	1.15	30	.44	38			.59	51	.29	25	113	6	
3.88	1.30	34	1.35	35	.42	32					.24	18		6	
3.88	1.18	30	1.40	36	.39	33					.24	20	71	7	
4.05	1.42	35	1.64	40	.47	33	.54	38	.69	49	.32	23	88	7	
4.05	1.32	33	1.59	39	.49	37			.66	50	.27	20			
4.05	1.42	35	1.49	37	.47	33	.44	31	.64	45	.34	24		7	
4.11	1.40	34	1.46	36			.61	44	.78	56	.42	30	82		
4.11	1.40	34	1.54	37	.44	31	.54	39	.86	61	.32	23		7	
4.11	1.30	32	1.35	33	.47	36	.44	34	.56	43	.27	21	77	7	
4.24	1.27	30			.44	35					.20	16		6	
4.24	1.35	32			.39	29					.32	24		6	
4.24	1.27	30	1.59	38	.44	35					.20	16	80	8	
4.24	1.37	32	1.67	39	.49	36			.64	47	.30	22		8	
4.30	1.30	30	1.42	33	.42	32	.47	36	.64	49	.32	25	71	6	
4.37	1.45	33	1.72	39	.47	32	.54	37	.66	46	.32	22	80	9+	
4.43	1.30	29			.42	32								7	
4.43	1.32	30	1.57	34	.47	36	.37	28	.61	46	.32	24	68	6	
4.43	1.35	30	1.54	35	.39	29	.39	29	.56	41	.20	15	80	7+	
4.43	1.59	36	2.08	47										14	
4.49	1.42	32			.47	33	.49	35	.66	46	.22	15		7	
4.56	1.45	32	1.64	36	.51	35							75	8	
4.62	1.45	31	1.59	34	.44	30	.47	32	.64	44	.34	23	77	7	
4.62	1.52	33	2.11	46	.54	36	.56	37	.73	48	.39	26		14	
4.62	1.59	34	1.89	41	.47	30			.73	54	.37	23		9	
4.62	1.47	32	1.76	38	.49	33			.69	47				8	
4.75	1.47	31	1.86	39	.54	37			.69	47	.27	18	77	8	
4.75	1.54	32	1.57	33	.47	31	.42	27	.56	36	.29	19	100	7	
4.75	1.42	30	1.59	33	.47	33	.39	27	.59	42	.22	15	88	6	
4.81	1.52	32	1.72	36	.49	32	.51	34	.71	47	.32	21	77	3	
4.81	1.79	37	1.98	41	.54	30	.61	34	.78	44	.39	22		14	
4.87	1.59	33	1.79	37	.49	31	.59	37	.69	43	.37	23	77	10	
4.87	1.47	30			.49	33					.32	22		8	
4.94	1.72	35	2.25	46	.56	33	.69	40	.81	47	.39	23			
4.94	1.52	31	1.72	35	.51	34	.51	34	.71	47	.24	16	125	8	
4.94	1.72	35	1.81	37	.49	28	.49	28	.64	37	.34	20	77	10	
4.94	1.52	31	1.64	33	.49	32	.49	32	.61	40	.32	21	85	11	
5.00	1.64	33	1.91	38										7	
5.06	1.67	33	1.96	39	.49	29	.51	31	.76	46	.49	29		10	
5.06	1.54	30	1.67	33	.47	31	.49	32	.64	42	.32	21		7	
5.06	1.59	31	1.72	34	.51	32	.51	32	.69	43	.32	20	80	8	
5.06	1.49	29	1.81	36	.49	33	.51	34	.66	44	.27	19		9	
5.19	1.64	32	1.96	38	.47	29	.61	37	.76	46	.39	24		12	
5.32	1.59	30	1.86	35	.49	31	.51	32	.66	42	.37	23		9	
5.32	1.62	30	1.74	33	.49	30	.54	33	.71	44	.34	21		8	
5.32	1.76	33	2.16	41	.54	31	.64	36	.81	46	.39	22	83	20	
5.44	1.81	34	2.33	43	.56	30	.66	36	.91	49	.47	26	85		
5.44	1.81	33	2.08	38	.54	30	.51	28	.69	38	.37	20	71	16	
5.44	1.72	32	1.94	37	.51	30	.66	38	.78	45	.44	26	77	16	
5.57	1.91	34	2.16	39	.54	28	.61	32	.78	41	.39	20	85	45	
5.89	2.08	35	2.45	42	.56	27	.69	33	.86	41	.47	23	83	20	15
6.01	1.89	31	2.13	35	.56	30	.69	37	.86	46	.56	30	75	50	25
6.01	1.89	31	2.13	35	.56	30	.61	32	.81	43	.51	27	85	53	35
6.08	1.84	30			.61	33	.52	28	.74	40	.37	20	92		
6.14	1.96	32	2.20	36	.49	25	.54	28	.74	38	.49	25	77	55	33
6.29	2.08	33	2.20	35	.49	24	.73	35	.81	39	.42	20	83	74	42
6.39	2.08	33	2.45	38	.59	28			.86	41	.49	24		56	38
6.39	2.20	34	2.87	45	.59	27	.73	33	.98	45	.56	25	81	68	42
6.50	2.07	32	2.60	40	.56	27	.64	31	.88	43	.47	23	88	55	
6.50	1.94	30	2.23	34	.56	29	.61	31	.78	40	.42	22			
6.70	2.20	33	2.35	35	.54	25	.64	29	.83	38	.44	20	68	58	35

See footnote at end of table.

TABLE 1.—*Selected measurements and counts of larval* Cyclopsetta fimbriata—Continued

Measurements												Counts	
Standard length	Head length (HL)		Body depth (BD)		Eye diameter (ED)		Upper jaw length (UJL)		Lower jaw length (LJL)		Snout length (SN)	Pelvic fin origin to tip of cleithrum [1] *blind-side* ocular-side	Dorsal fin rays	Anal fin rays
Mm.	*Mm.*	*HL / SL*	*Mm.*	*BD / SL*	*Mm.*	*ED / HL*	*Mm.*	*UJL / HL*	*Mm.*	*LJL / HL*	*Mm.*	*SN / HL*	*Percent*	*Number*	*Number*
6.70	2.08	31	2.72	41	0.64	31	----------		0.78	38	0.42	20	69	64	44
6.80	2.08	31	2.45	36	.49	24	----------		.86	41	.42	20	100	----------	----------
6.91	2.16	31	2.45	35	.56	26	.71	33	.93	43	.42	19	77	----------	39
7.01	2.20	31	2.72	39	.56	25	.74	34	.93	42	.56	25	83	73	50
7.01	2.28	33	2.83	40	.61	27	.81	36	.98	43	.49	21	78	66	46
7.53	2.38	32	2.83	38	.69	29	.81	34	1.03	43	.56	24	75	----------	----------
7.63	2.38	31	3.03	40	.66	28	----------		1.03	43	.59	25	84	72	50
8.04	2.56	32	3.22	40	.69	27	.93	36	1.10	43	.61	24	88	79	62
8.04	2.64	33	3.14	39	.74	28	.91	34	1.10	42	.59	22	83	----------	----------
8.25	2.83	34	3.49	42	.74	26	1.00	35	1.22	43	.74	26	88	----------	----------
8.76	2.91	33	3.69	42	.71	24	1.00	34	1.15	40	.66	23	71	79	56
9.18	2.79	30	3.30	36	.69	25	----------		----------		.69	25	74	81	57
9.38	3.38	36	4.30	46	.71	21	1.00	30	1.35	40	.86	25	71	79	60
9.38	2.95	31	3.80	41	.74	25	1.03	35	1.22	41	.74	25	78	82	63
9.59	3.49	36	4.24	44	.69	20	1.00	29	1.30	37	.81	23	92	77	54
9.79	2.91	30	3.61	37	.71	24	.91	31	1.18	41	.74	25	65	76	60
10.21	3.03	30	4.11	40	.66	22	.98	32	1.15	38	.73	24	71	81	61
10.31	3.65	35	4.62	45	.81	22	----------		1.52	42	.88	24	69	77	58
10.31	3.10	30	4.24	41	.71	23	1.10	36	1.35	44	.73	24	61	78	60
10.31	3.18	31	4.11	40	.74	23	1.10	35	1.32	42	.74	23	74	79	59
11.08	3.57	32	4.43	40	.78	22	1.15	32	1.42	40	.91	25	100	82	62
12.06	3.80	32	4.56	38	.86	23	.98	26	1.35	36	.86	23	79	77	58
12.23	3.99	33	4.89	40	.91	23	1.32	33	1.71	43	.91	23	78	82	58
13.20	4.49	34	5.38	41	.86	19	1.42	32	1.84	41	1.18	26	73	82	61
13.53	4.18	31	5.25	39	.93	22	1.35	32	1.72	41	.98	22	82	84	61
13.86	4.30	31	----------		.91	21	1.25	29	1.71	40	.98	23	65	----------	----------
14.02	4.62	33	5.51	39	.98	21	1.59	34	1.98	43	1.05	23	92	80	60
14.18	4.75	33	6.01	42	.93	20	1.49	31	2.03	43	1.22	26	73	83	61
14.51	4.75	33	5.87	40	1.22	26	1.40	29	1.84	39	1.10	23	78	80	58

[1] Distance between the origin of the right side pelvic fin base and the tip of the cleithrum divided by the distance between the origin of the left side pelvic fin base and the tip of the cleithrum.

TABLE 2.—*Average values for selected measurements and counts (½-mm. size intervals to 5.0 mm. SL; 1-mm. intervals for larger sizes); all specimens in a given size series were not necessarily used to compute the mean*

Measurements															Counts	
Standard length		Specimens	Head length (HL)		Body depth (BD)		Eye diameter (ED)		Upper jaw length (UJL)		Lower jaw length (LJL)		Snout length (SN)		Pelvic fin origin to tip of cleithrum [1] *blind-side* ocular-side	Dorsal fin rays	Anal fin rays
Range	*Mean*		*Mean*	*HL / SL*	*Mean*	*BD / SL*	*Mean*	*ED / HL*	*Mean*	*UJL / HL*	*Mean*	*LJL / HL*	*Mean*	*SN / HL*			
Mm.	*Mm.*	*Number*	*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Percent*	*Number*	*Number*
1.50–1.99	1.79	4	0.50	28	0.52	29	0.21	40	----------		----------		0.09	17	----------	----------	----------
2.00–2.49	2.20	6	.69	32	.64	32	.28	40	----------		----------		.12	16	----------	3.8	----------
2.50–2.99	2.80	18	.83	30	.84	30	.32	38	0.28	33	0.41	49	.13	16	93	3.4	----------
3.00–3.49	3.28	23	1.06	32	1.12	34	.38	37	.37	35	.50	47	.21	20	92	5.2	----------
3.50–3.99	3.68	15	1.25	34	1.42	39	.42	34	.49	38	.60	48	.29	23	85	6.6	----------
4.00–4.49	4.25	17	1.37	32	1.59	37	.44	33	.48	35	.66	48	.29	21	78	7.5	----------
4.50–4.99	4.78	16	1.55	32	1.79	38	.50	32	.52	33	.68	44	.33	21	86	12.1	----------
5.00–5.99	5.30	16	1.70	32	1.98	38	.51	30	.57	33	.75	44	.39	23	81	14.3	15.0
6.00–6.99	6.42	13	2.04	32	2.40	37	.56	28	.64	32	.84	41	.46	23	81	54.8	37.0
7.00–7.99	7.30	4	2.31	32	2.85	39	.63	27	.79	35	.99	43	.55	24	80	70.3	48.6
8.00–8.99	8.27	4	2.74	33	3.38	41	.72	26	.96	35	1.14	42	.65	24	82	79.0	59.0
9.00–9.99	9.46	5	3.10	33	3.85	41	.71	23	.98	31	1.26	40	.77	25	76	79.0	58.8
10.00–10.99	10.28	4	3.24	32	4.27	42	.73	22	1.06	34	1.34	42	.77	24	69	78.8	59.5
11.00–11.99	11.08	1	3.57	32	4.43	40	.78	22	1.15	32	1.42	40	.91	25	100	82.0	62.0
12.00–12.99	12.14	2	3.90	32	4.72	39	.88	23	1.15	30	1.53	40	.88	23	78	79.5	58.0
13.00–13.99	13.53	3	4.32	32	5.32	40	.90	21	1.34	31	1.76	41	1.05	24	73	83.0	61.0
14.00–14.99	14.24	3	4.71	33	5.80	40	1.04	22	1.49	31	1.95	42	1.12	24	81	81.0	59.7

[1] Distance between the origin of the right side pelvic fin base and the tip of the cleithrum divided by the distance between the origin of the left side pelvic fin base and the tip of the cleithrum.

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CONTROL OF OYSTER DRILLS, EUPLEURA CAUDATA *AND* UROSALPINX CINEREA, *WITH THE CHEMICAL POLYSTREAM*

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ABSTRACT

Five experimental and 10 commercial treatments of oyster beds in four States were made with Polystream. On a typical bed, where water currents were less than 2.7 km. per hour, Polystream killed about 85 percent of the thick-lipped drill, *Eupleura caudata*, and 66 percent of the Atlantic oyster drill, *Urosalpinx cinerea*. A significantly higher percentage of oyster drills was killed by treatments made in late April and early May rather than later in the summer. Oyster drills that survived did not feed for several months. The number of drills remained low for at least 2 years. Polystream treatments killed only small percentages of fish, small clams, *Mercenaria mercenaria*, crabs, and other invertebrates. After a treatment, oysters, *Crassostrea virginica*, clams, and other organisms had small residues of Polystream in their tissues but gradually lost these residues. Growth of oysters was normal on treated beds.

Boring gastropods, known as oyster drills, and starfish, *Asterias forbesi*, are the most serious predators of oysters in Long Island Sound. The drills prey heavily on oysters, *Crassostrea virginica*, along the entire Atlantic Coast, from Canada to Florida, and in certain areas of the Pacific Coast. Where they are extremely numerous, oyster drills destroy nearly all oysters on commercial beds. In Long Island Sound, however, drills usually reduce the number of oysters to such a level that most beds are of marginal value commercially.

This article summarizes laboratory and field experiments made during the development of a control method of oyster drills for use on commercial oyster beds in southern New England and New York; it includes the results of 15 treatments during 1961–67.

HISTORY OF DEVELOPMENT OF METHOD

All early phases of work on the development of a method of control of oyster drills by use of Polystream, including the initial testing of chemicals, was done by the biological laboratory at Milford, Conn. Field tests and commercial applications of Polystream were made under the inspection of the author in the States of Connecticut, New York, Rhode Island, and Massachusetts. Additional independent laboratory and field studies were later made in Virginia.

EXPERIMENTAL WORK AT MILFORD

In 1946, the Fish and Wildlife Service biological laboratory, Milford, Conn., began a program of screening organic chemicals with the goal of eventually developing a method to control oyster drills (Loosanoff, 1960). A method was sought that would kill oyster drills, but would not harm oysters, clams, *Mercenaria mercenaria*, and other organisms on a shellfish bed, and also would not leave residues in tissues of shellfish that would be harmful to man. Tests were made in the laboratory and the field.

Laboratory Tests

Loosanoff, MacKenzie, and Shearer (1960a, 1960b) reported that chlorinated benzenes, such as monochlorobenzene, orthodichlorobenzene, paradichlorobenzene, trichlorobenzene, tetrachlorobenzene, and their mixtures, are toxic to several species of marine gastropods, including the thick-lipped drill, *Eupleura caudata*, and the Atlantic oyster drill, *Urosalpinx cinerea*. These chemicals were selected for further tests because they were toxic to snails, virtually insoluble in sea water, and of sufficient density to settle to the bottom of the Sound. The last two characteristics reduced the chance of damage to any but bottom-dwelling organisms whose soft parts contact the chemicals directly. Small quantities of Sevin (1-naphthyl-

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N-methylcarbamate) were added to the chlorinated benzenes to increase their killing effect on the snails. In laboratory experiments, orthodichlorobenzene mixed with dry sand in the ratio of 1 to 19, by volume, and then spread over shallow pans killed most oyster drills; and when used to form a barrier in small troughs it prevented them from crossing the barrier for several months.

Loosanoff, MacKenzie, and Davis[1] stated that for 14 months small barriers consisting of orthodichlorobenzene and sand continued to affect oyster drills on contact but were not toxic to larvae and juveniles of sea squirts, *Molgula manhattensis*, common shipworms, *Teredo* sp., Atlantic oyster drills, eastern white slippers, *Crepidula plana*, and mud blister worms, *Polydora* sp., which set and grew within 2.5 cm. (1.0 inch) of the barriers. These observations showed that orthodichlorobenzene was only a contact poison. In large outdoor troughs siltation reduced the effectiveness of chlorinated benzenes by forming a covering layer that kept the oyster drills from touching the chemicals.

Field Tests

Loosanoff (1961) reported that oyster drills can be greatly reduced in numbers by spreading chemically treated sand over shellfish beds. The combination that gave good results consisted of 95 percent dry sand and 5 percent orthodichlorobenzene containing 1 to 3 percent, by weight, of Sevin. The chemicals were mixed with the sand in large commercial cement trucks. The treated sand, loaded on the deck of a boat, was then spread over the oyster bed by a high-pressure stream of water.

Davis, Loosanoff, and MacKenzie[2] reported the results of treatments of several small oyster beds. They emphasized the effects of chemical treatments on organisms other than oysters and clams. On July 16, 1961, a bed of about 1.6 ha. (4 acres) in Great South Bay, Long Island, N.Y., was treated with 9.5 kl. per hectare (5 yards per acre) of sand mixed with 1.9 hl. (50 gallons) of orthodichlorobenzene containing 6 kg. (13 pounds) (2 percent by weight) of Sevin. As the sand descended, several small fish were killed and common jellyfish were carried to the bottom. Shortly after the sand reached the bottom, sea squirts were found partially contracted; oyster drills and other snails were greatly swollen; and a number of hermit crabs, *Pagurus* sp., and mud crabs, *Neopanope texana*, were dead. They did not determine whether this experimental treatment eventually killed the oyster drills. Another bed, which was off the east end of Long Island in 9 m. of water, was treated in like manner. Because of strong water currents over the area, little sand actually reached the bottom that was to be treated and, as a result, the treatment was not effective. This failure indicated that in an area with strong currents it was very difficult to control oyster drills with sand treated with a chlorinated benzene.

In treatments along the Connecticut shore the effects of the chemicals on animals inhabiting the bottom varied somewhat depending on location of the bed. In open waters, divers noticed only a small effect on fish, hermit crabs, mud crabs, and annelids. In areas where waters were shallower and currents slower, however, the effect was greater. In all tests, fish, hermit crabs, and mud crabs fed and moved normally in an area within a few days after a treatment. Fish, perhaps attracted by the exposed white feet of swollen gastropods, were more numerous after a treatment. Most pelagic common shrimp that were in the immediate area at the time the treated sand was spread were apparently killed. Once the chemicals were on the bottom, however, shrimp moved in again and remained uninjured. Oysters and mussels, *Mytilus edulis*, when present, were pumping normally within an hour of the treatment. Starfish, *Asterias forbesi*, were irritated by treated sand falling on their aboral surface, and small sores soon appeared. In a number of treated areas starfish consumed swollen oyster drills and northern moon shells, *Polinices* sp. Davis et al.[3] also reported that the treatment did not reduce the intensity of setting of oyster and starfish larvae in the area.

Polystream[4] (trademark of Hooker Chemical Corporation for a mixture of polychlorinated benzenes containing a minimum of 95 percent total of active trichlorobenzene, tetrachlorobenzene, and

[1] Loosanoff, V. L., C. L. MacKenzie, Jr., and H. C. Davis. 1960. Progress report on chemical methods of control of molluscan enemies. Bur. Commer. Fish. Biol. Lab., Milford, Conn., Bull. 24 (8), 20 pp.

[2] Davis, H. C., V. L. Loosanoff, and C. L. MacKenzie, Jr. 1961. Field tests of a chemical method for the control of marine gastropods. Bur. Commer. Fish. Biol. Lab., Milford, Conn., Bull. 25 (3), 9 pp.

[3] See footnote 2.

[4] Trade names referred to in this publication do not imply endorsement of commercial products.

pentachlorobenzene, and having a last crystal point of 18° C. ± 3° C.), a less expensive product than orthodichlorobenzene, was used for the first time on experimental beds in New Haven Harbor, Conn., in the summer of 1961. I made field tests to compare the effectiveness of orthodichlorobenzene and Polystream and to determine the minimum quantity of chemically treated sand needed to control oyster drills. Sevin was added to both types of polychlorinated benzenes at the rate of 2 percent by weight, and a total of 1.9 hl. of either orthodichlorobenzene or Polystream was mixed with each 9.5 kl. of sand. The two chemical-sand mixtures were spread over eight 0.4-ha. beds at rates of 1.9, 5.1, 9.5, and 19 kl. per hectare. Drill traps were used to estimate the effects of treatments on populations of oyster drills and mud crabs.

SCUBA divers studied the effects of these treatments. Their observations indicated that treatments of 9.5 and 19.0 kl. per hectare of either orthodichlorobenzene and Sevin or Polystream and Sevin caused all visible gastropods, including thick-lipped drills, northern moon shells, knobbed whelks, *Busycon carica*, channeled whelks, *Busycon canaliculatum*, and New England nassas, *Nassarius trivittatus*, to become swollen (snails listed in order of importance as shellfish predators; the New England nassa is not a predator). Apparently, the latter three species of predators were compelled to emerge from their usual position buried in the bottom. A number of pipefish, *Syngnathus fuscus*, mud crabs, and shrimp were either partially paralyzed or behaved abnormally. Small flounders, *Pseudopleuronectes americanus*, however, swam around apparently unharmed. Three days later these effects were more evident; all visible gastropods were either swollen and being eaten alive by starfish or they had already died. The pipefish, mud crabs, and shrimp, nevertheless, had either recovered or had been replaced by others from surrounding areas. Subsequent observations revealed that starfish were gradually consuming the remaining swollen gastropods. Thus, the area was left with a large number of empty gastropod shells which gradually disappeared; a lot with 42 shells of the northern moon shell per 50 m.^{2} of bottom on July 3, for example, had none by July 18. Presumably, the shells had been occupied by hermit crabs and carried away.

Catches of oyster drills on traps indicated that applications of 9.5 and 19.0 kl. of treated sand per hectare had killed nearly all drills and that the mixture of Polystream and Sevin was more effective than the mixture of orthodichlorobenzene and Sevin. The numbers of mud crabs on traps before and after treatments indicated that they were not harmed by the treatments. As a result, we thereafter used Polystream exclusively, abandoned orthodichlorobenzene, and standardized the treatment rate at 9.5 kl. per hectare.

Increased catches of drills, along the borders of lots several weeks after the treatment, indicated that drills were migrating into the lots from surrounding areas. This observation suggested that to ensure protection of an oyster bed from oyster drills, a zone perhaps 25 or more meters wide outside the bed, as well as the bed itself, should be treated, and that treatment of a single large bed would be more efficient than treatment of a number of small beds.

Polystream was used to treat beds inhabited by oysters and clams that are later consumed by humans. It was necessary, therefore, to determine whether these shellfish retained any residues of this chemical. In practice, however, only those beds with seed oysters on them are treated with Polystream. These oysters are transplanted to untreated beds at least 4 months before harvest. It was also desirable to know whether other organisms inhabiting treated beds, particularly those that might be taken by sport or commercial fishermen, retain residues of Polystream.

To determine whether oysters, clams, or other animals or plants accumulated and then lost residues of Polystream, I studied specimens that were collected from treated beds by divers or by dredging. I also studied northern lobsters, *Homarus americanus*, in cages to determine whether residues would be lost after a period of time in water free of Polystream. The U.S. Testing Company of Hoboken, N.J., determined the quantity of Polystream in tissues of the plants and animals through use of a technique developed by Schwartz, Gaffney, Schmutzer, and Stefano (1963).

In 1961 and 1962, I determined the quantities of Polystream in oysters and clams from a 0.4-ha. lot, treated with 1.9 hl. of this chemical. In oysters the residue was 1.8 p.p.m. (parts per million) 8 days after the treatment. It diminished slowly until none was detected 119 days later. Residues in clams

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TABLE 1.—*Residues of Polystream in oysters and clams on a 0.4-hectare bed in New Haven Harbor, Conn., after it was treated with Polystream-sand, June 27–29, 1966*

Time after treatment	Residues	
	In oysters	In clams
Days	*P.p.m.*	*P.p.m.*
8	1.8	1.1
14	2.3	1.7
28	0.2	0.6
56	0.3	0.3
77	0.7	0.7
119	<0.1	<0.1
336	<0.1	<0.1
455	0.1	0.1

were at similar levels and were lost at similar rates (table 1).

Oysters removed from a treated bed and replanted on an untreated area lost any residue of Polystream within a week. Nevertheless, the first few times oysters that had once grown on a treated bed were to be harvested, they were analyzed for any possible residue of Polystream before clearance for marketing. None of these oysters had residues.

In 1966, I determined the rates of loss of Polystream in oysters at several distances from lot 42, Norwalk, which was treated on August 24, 1966, and where strong currents had washed many granules off the lot. After 8 days, residues were as high as 0.3 p.p.m. in oysters 150 m. from the lot and were higher in oysters closer to the lot. On October 13, however, only those oysters 15 m. or closer to the lot showed any residue. At this distance the level had dropped from 1.7 p.p.m. in September to 0.2 p.p.m. On December 8, 106 days after the treatment, no residues were detected in any oysters outside the treated lot (table 2).

To determine the quantity of Polystream in tissues of other organisms inhabiting an oyster bed,

TABLE 2.—*Residues of Polystream in oysters collected at various distances from lot 42, Norwalk, Conn. Lot was treated on August 24, 1966*

Distance from lot 42	Date of collection (1966)		
	Sept. 1	Oct. 13	Dec. 8
M.	*P.p.m.*	*P.p.m.*	*P.p.m.*
15	1.7	0.2	<0.1
30	0.4	<.1	<.1
75	0.2	<.1	<.1
150	0.3	<.1	<.1

I made periodic collections from treated beds. All species of animals or plants collected within a year had accumulated a small quantity of Polystream. Residues of Polystream eventually diminished in those species, namely, the bay scallop, *Pecten irradians*, hermit crab, and sea lettuce, *Ulva* sp., where comparisons between time intervals were made (table 3).

By holding northern lobsters in a cage for a week in the center of a bed 45 days after it was treated, I found that they do accumulate a small residue of Polystream (1.4 p.p.m.) when retained in a treated area. A group of lobsters held on the treated lot for a week and then held on an untreated area for another week did not have any residue. Thus, lobsters may accumulate a small quantity of Polystream while they inhabit a treated bed, but they lose it soon after they leave the bed.

To determine mortality rates of oysters because of possible predation by oyster drills on treated beds, divers collected oysters periodically on several beds. The divers either swam across the center of beds for a distance of perhaps 150 m., gathering about 30 clusters of oysters randomly, or they collected oysters and all other material from within a metal ring enclosing either 1 or 1.5 $m.^2$ of bottom from 10 different sections.

TABLE 3.—*Residues of Polystream in animals and plants inhabiting oyster beds in Conn. and N.Y. treated with Polystream*

Animal or plant	Location	Time after treatment	Residue
		Days	*P. p.m.*
Northern puffer (*Sphaeroides maculatus*)	New Haven (State spawning bed)	31	5.9
Sea robin (*Prionotus carolinus*)	New Haven (State spawning bed)	25	8.4
Sand shark (*Carcharias taurus*)	New Haven (lot 152)	8	5.0
Starfish (*Asterias forbesi*)	New Haven (lot 15)	30	1.8
Bay scallop (*Pecten irradians*)	Sag Harbor (lot 8)	6	13.6
Bay scallop	Sag Harbor (lot 8)	250	0.9
Northern moon shells (*Polinices* sp.)	Northport (lot 1)	1 hour	50.0
Hermit crab (*Pagurus* sp.)	New Haven (lot 152)	1	12.3
Hermit crab		25	2.2
Mud crab (*Neopanope texana*)	New Haven (lot 152)	1	20.5
Red sponge (*Microciona prolifera*)	New Haven (lot 13)	25	2.3
Spaghetti grass (*Codium fragile*)	Sag Harbor (lot 8)	250	0.1
Sea lettuce (*Ulva* sp.)	New Haven (lot 152)	1	8.9
Sea lettuce	Sag Harbor (lot 8)	6	0.3

EXPERIMENTAL RESULTS IN OTHER AREAS

Wood and Roberts (1963) reported that in the laboratory Polystream alone killed 50 to 78 percent of large Atlantic oyster drills from the Eastern shore of Virginia and that a mixture of Polystream and Sevin killed 66 to 77 percent. Thus, they felt that Sevin was not needed. They also indicated that if oyster drills are in poor condition, they are more easily killed by Polystream. Therefore, they recommended that treatments should be made in the early spring when oyster drills are emerging from winter dormancy.

Haven, Castagna, Chanley, Wass, and Whitcomb (1966) reported the results of a field test in Hog Island Bay, Va. A 0.4-ha. section of bottom was treated with 9.5 kl. of sand mixed with Polystream containing 2 percent of Sevin. The oyster drills were not killed by the treatment, they deposited egg cases at a normal rate, and they destroyed as many oysters on the treated plots as on untreated control plots. I believe the reason for the ineffectiveness was that the treated sand soon sank as deep as 4 cm. into a layer of silt on the bed; thus, the drills could move over the bottom without contacting significant quantities of the chemicals. Haven et al. (1966) also reported that the Polystream-Sevin treatment had a deleterious effect on other living organisms and that growth of oysters and clams was apparently retarded.

RESULTS OF COMMERCIAL TREATMENTS

I used several methods to evaluate the effectiveness of treatments in killing oyster drills and their effects on organisms inhabiting oyster beds. Ten commercial treatments of oyster beds are described.

METHODS USED IN EVALUATION

Oyster companies used a standard rate of 1.9 hl. of Polystream per hectare (50 gallons per acre) of oyster bed. In early treatments, they mixed Sevin with Polystream at the rate of 2 percent by weight. The Polystream was mixed with either dry sand or a granular clay [the mixture is termed Polystream (Granular)] which carried it to the bottom and dispersed it.

Several techniques were used to evaluate the effects of treating commercial oyster beds with Polystream and Sevin. On numerous occasions SCUBA divers examined each bed carefully for 20 to 30 minutes to determine the gross effects of the chemicals on all visible living animals and plants. Often they made the first examination within an hour of a treatment and followed it by many subsequent periodic examinations during the next 2 to 3 years. They examined certain beds once a month during collections to determine survival rates of oysters.

In 1961–63, drill traps were used to estimate the effectiveness of treatments in controlling oyster drills. Because mud crabs enter drill traps in large numbers, I estimated the effect of treatments on these populations.

From 1964–67 I made quantitative determinations of the number of drills per unit area with a hydraulic sampler, which pumps through a mesh bag all bottom material from within a ring enclosing areas of 1 or 1.5 m.^{2} All coarse material is retained within the bag, carried to the surface, and sorted. This sampling method, which is carried out by divers, provides an accurate measure of the density of oyster drills and other mollusks on a shellfish bed if enough samples are taken. I took about 25 random samples on beds 2 to 6 ha. in size a few days before and again about a month after a treatment. I determined the percentage of oyster drills killed by comparing their densities before and after treatments. Actually, the Atlantic oyster drills on many beds were too few in number for me to determine the precise percentage of this species killed.

EFFECTS OF TREATMENTS IN DIFFERENT AREAS

Ten commercial treatments in four States were made with Polystream. Each treatment will be described separately by areas.

Area 1: Lewis Gut, Bridgeport, Conn., 1962

Lewis Gut is a long narrow arm of Bridgeport Harbor. The water is about 1 to 3 m. deep at low tide, and maximum currents run at about 4.5 km. per hour (2.5 knots). On June 27 and 29, 1962, an oyster company treated 12 ha. of this area with a mixture of Polystream-Sevin and sand.

Effect on gastropods.—Divers observed that within an hour after the treatment nearly all thick-lipped drills, Atlantic oyster drills, northern moon shells, and both knobbed and channeled whelks

were swollen; a few weeks later most of these gastropods, as well as mud snails, were dead.

To evaluate the number of oyster drills killed, I used drill traps. The catch per trap per week fell from 16 drills before the treatment to 0.4 drill afterwards. One year later the average catch of oyster drills increased, primarily by recruitment of young drills, to about two per trap per week. In 1964, the average catch rose to about 5 per trap per week, again as a result of recruitment by young oyster drills; by July 1965 it rose to 13 per trap per week (fig. 1).

Effect on associated animals.—During 1961, divers observed that only a small number of fish—primarily sea robins, *Prionotus carolinus;* pipefish; flounders; mummichogs, *Fundulus heteroclitus;* and eels, *Anguilla rostrata*—were present in Lewis Gut before or after the treatment. Immediately after the application of chemicals only the pipefish appeared to be affected, i.e., more sluggish than usual. A few hours later, however, mummichogs were dying along the shore as some of the finer sand coated with Polystream was churned up in the water by wave action.

This treatment had a slight effect on several organisms. Hermit crabs were affected to some degree. A number of them had no shells; apparently, a small quantity of treated sand entered the shell and caused enough irritation to compel them to leave. The abdomens of a number of these crabs had been bitten off. Most mud crabs were unaffected, but between 5 and 10 percent were twitching abnormally immediately after the treatment. The treatment also compelled many nereids and nemerteans to emerge from their burrows. A few weeks later all animals not killed by the initial treatment appeared to be normal.

Catches on drill traps indicated that the treatment did not reduce the population of mud crabs. The weekly catch of these crabs on drill traps followed the same pattern each year: Each trap caught an average of about 15 crabs per week in May, June, and July; about 10 crabs during August; and (because of recruitment of young crabs) 18 to 23 crabs in the fall (fig. 2).

Effect on predation.—In midsummer of 1962 an oyster company planted 3,500 hl. (10,000 bushels) of seed oysters in Lewis Gut. Periodic examination of the oysters through early winter showed little loss from predation by oyster drills.

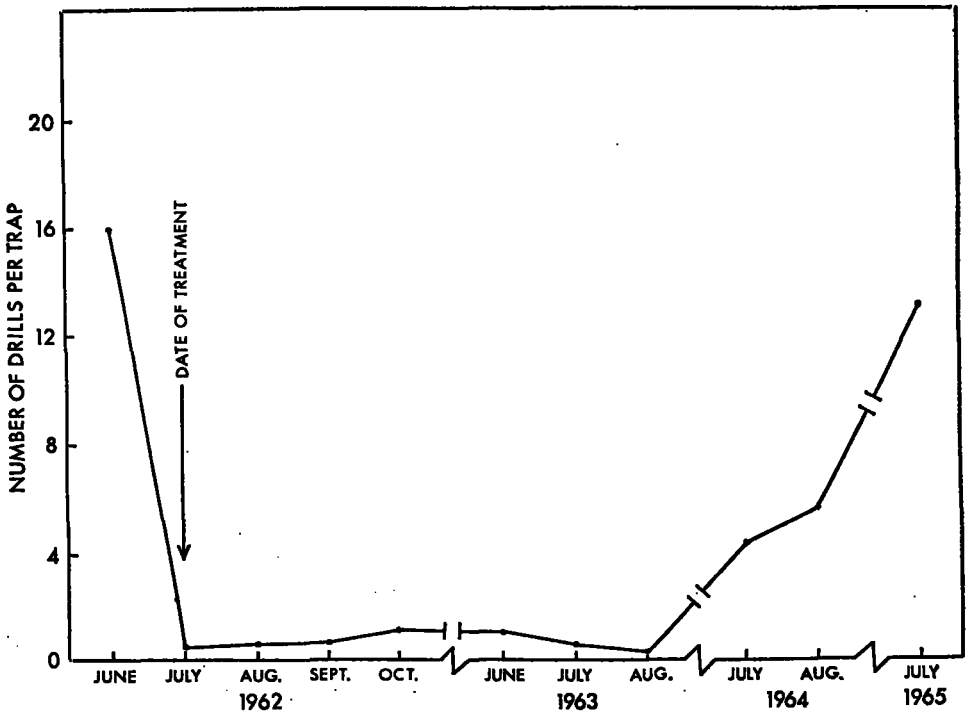

FIGURE 1.—Catches of oyster drills on traps in treated area of Lewis Gut, Bridgeport, Conn.

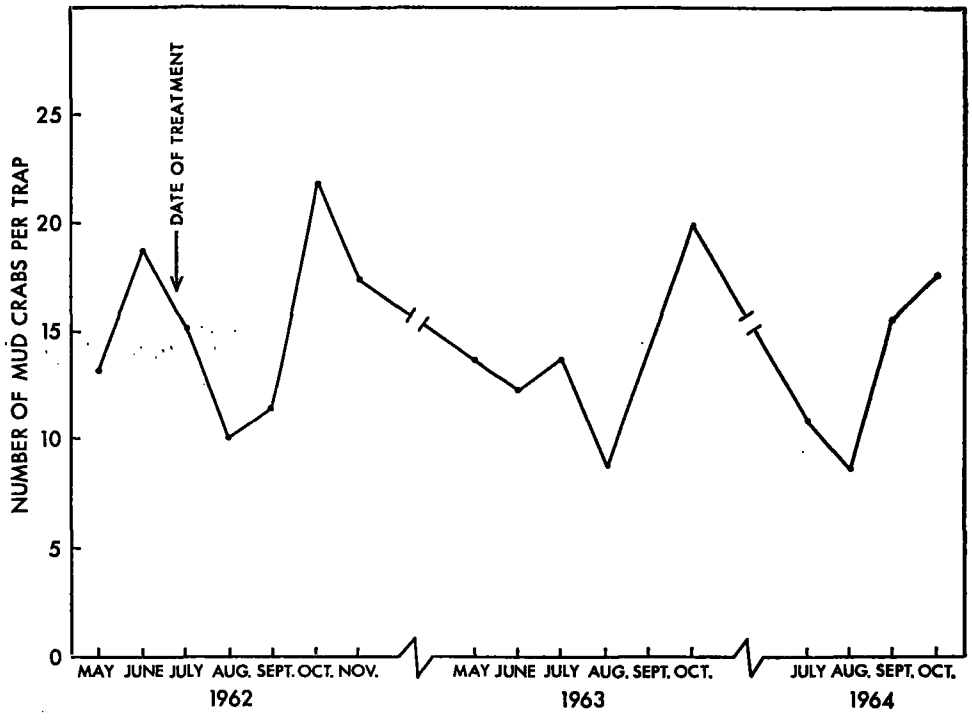

FIGURE 2.—Catches of mud crabs on traps in treated area of Lewis Gut, Bridgeport, Conn.

Area 2: Northport Harbor, N.Y., 1963

Northport Harbor on the north shore of Long Island is about 6.5 km. long. The oyster beds are in water 4.5 to 7.5 m. deep at low tide, and water currents rarely exceed 1.8 km. per hour.

On May 21 and 28, 1963, I made a series of comparative treatments. The purpose was to determine whether Drillex (a mixture of Polystream and 2 percent by weight of Sevin) is more lethal to oyster drills than Polystream alone. The experiment had four 2-ha. lots. Two lots received an application of 11.5 kl. of treated sand per hectare. They were designated as 1 (for Polystream) and 1 x (for Drillex). The remaining two lots which received 19.0 kl. of treated sand per hectare were designated as 2 and 2 x.

Effect on gastropods.—The treatments had a very deleterious effect on gastropods. A few hours after the treatments, divers observed that nearly every visible gastropod on all four lots was swollen; on lots treated with Drillex, however, the drills expanded faster and sooner. Ten days after the treatments, most thick-lipped drills were drawn deeply into their shells but some were still swollen. Northern moon shells were observed in three conditions—partially expanded, dormant with their operculum flush with their aperture, and dead. Twenty-three days after the treatments divers noted that all visible thick-lipped drills were dead on lots 2 and 2 x, and only a small number were alive on lots 1 and 1 x. No northern moon shells were observed either dead or alive; even their shells were gone. Hermit crabs had probably carried them off the bed.

Because many flounders were swimming over the beds and crabs were numerous when the snails were swollen, these fish had ample opportunity to feed on the paralyzed drills. I observed no snails being consumed, however; instead, they appeared to die directly from the toxic effects of the chemicals.

Examination of the bottom showed that Polystream alone killed almost as many oyster drills as Drillex.

Effect on associated animals.—Divers observed that during the applications of Drillex-sand a small number of flounders, many hermit crabs, shrimp, and annelids were killed; however, 10

days later they saw a large number of healthy flounders (only about 1 percent were still affected) and mud crabs on the two treated beds.

Polystream was used in all later commercial treatments because these experiments showed it was much less toxic than Drillex to associated animals, particularly arthropods.

Effect on predation.—I made no careful quantitative determinations; however, periodic observations of the lot indicated that predation by oyster drills on oysters on the treated lots during 1963 was slight.

Area 3: Northport Harbor, N.Y., 1965

On April 28, 1965, which was 2 years after the initial treatment, lot 1 was treated again with Polystream-sand.

Effect on gastropods.—Eight days after the treatment divers observed that every snail was swollen.

The treatment killed 64 percent of the oyster drills (77.2 percent of the thick-lipped drills and 8.6 percent of the Atlantic oyster drills) and reduced their numbers from 31.5 to 11.4 per m.[2] (table 4).

Effect on associated animals.—Nine days after the treatment divers found 6 stunned adult flounders and one dead juvenile on the bed among about 50 healthy flounders of mixed ages. The only hermit crab they saw was healthy.

Before treatment the number of young clams (5–7 mm. long) on the bed was 158 per square meter; 28 days after the treatment the number of clams was 125 per square meter. Thus, apparently only about 20 percent were killed.

Effect on predation.—I made no quantitative determinations. Periodic observations of the lot indicated, however, that predation by oyster drills during 1965 was slight.

Area 4: Northport Harbor, N.Y., 1966

On May 9, 1966, 3 years after the initial treatment, lot 2 was treated again, this time with Polystream (Granular).

Effect on gastropods.—Three days after the treatment divers found that all thick-lipped drills, Atlantic oyster drills, northern moon shells, and New England nassas were swollen.

The treatment killed 92 percent of the oyster drills (94.5 percent of the thick-lipped drills and 71.7 percent of the Atlantic oyster drills) and reduced their numbers from 27 to 2.1 per square meter (table 4).

Effect on associated animals.—No observations were made by divers.

Effect on predation.—I made no careful quantitative determinations. Several observations of the lot indicated, however, that predation by oyster drills during 1966 was slight.

TABLE 4.—*Density of oyster drills, before and after treatments with Polystream and sand or Polystream (Granular), on oyster lots in N.Y., Conn., R.I., and Mass., 1965–67*

Lot no. and area [1] (hectares)	Date of treatment	Formulation	Drills per m.[2]				Killed [4]		
			Before treatment		After treatment		*E. caudata*	*U. cinerea*	Both species combined
			E. caudata	*U. cinerea*	*E. caudata*	*U. cinerea*			
			Number	*Number*	*Number*	*Number*	*Percent*	*Percent*	*Percent*
25 (3.2)	4/30/65	Poly-sand	3.3	0.9	0.0	0.5	100.0	46.6	88.7
1 (2.4–3.2)	4/28/65	Poly-sand	25.2	6.3	5.7	5.7	77.2	8.6	64.0
2 (2.0)	5/9/66	Poly (Gran.)	24.1	2.9	1.3	0.8	94.5	71.7	92.3
205 (1.6)	9/15/66	Poly (Gran.)	[3] 4.0		[3] 0.9				77.5
18 [3]	4/ ?/67	Poly (Gran.)	7.5	0.9	2.4	1.6	68.0		52.0
40 [3]	4/29/67	Poly (Gran.)	12.0	4.7	2.2	1.6	82.2	66.7	77.8
49 [3]	4/29/67	Poly (Gran.)	5.6	0.7	0.9	0.0	84.6	100.0	86.4
42 (2.8)	5/ 1/67	Poly (Gran.)	3.0	0.3	0.9	1.0	66.7		43.5
50 [3]	5/ 1/67	Poly (Gran.)	12.6	1.3	1.7	0.6	86.4	55.6	83.5
19	Control	None	18.8	0.7	19.5	1.7			
RI (0.8)	5/ 1/67	Poly (Gran.)	0.0	6.5	0.0	0.0		100.0	100.0
FP (0.08)	5/29/67	Poly (Gran.)	0.0	40.8	0.0	2.2		94.5	94.5
FP	Control	None	0.0	37.2	0.0	33.2			

[1] Lot 25, Oyster Bay, N.Y.; Lots 1, 2, Northport, N.Y.; Lots 205, 18, 40, 49, 42, 50, and 19, Norwalk, Conn.; RI, Charlestown Pond, R.I.; FP, Fresh Pond Mass.

[2] Actual number of hectares treated on these beds is unknown, but I estimated that areas treated ranged between 1.2 and 6.0 hectares.

[3] Both species.

[4] If count increased, no percentage is given for this species

Area 5: Sag Harbor, N.Y., 1963

A 0.4-ha. lot along the eastern shore of Shelter Island in Sag Harbor was treated. The water over this lot is about 3 m. deep at low tide, and maximum currents are about 2.7 km. per hour.

On September 27, 1963, Polystream (Granular) was used for the first time to control oyster drills.

Effect on gastropods.—Within an hour of the treatment divers noticed that all visible snails were at least partially swollen. A week later divers observed many affected thick-lipped drills, Atlantic oyster drills, northern moon shells, and both knobbed and channeled whelks.

Ten drill traps were placed on the treated lot and an adjacent area before the treatment. The traps in each area collected between 200 and 300 oyster drills. After the treatment, traps were examined only once. They collected only 10 oyster drills on the treated area but gathered 127 on the control area. I did not count the two species of drills separately.

Effect on associated animals.—Divers observed that the treatment did not affect associated animals and plants, such as flounders, bay scallops, mud crabs, and sea lettuce.

Effect on predation.—No determinations were made.

Area 6: Oyster Bay Harbor, N.Y., 1965

Oyster Bay Harbor on the north shore of Long Island is about 8 km. long. The oyster beds are in water from 3.5 to 10 m. deep at low tide and water currents do not exceed 2.7 km. per hour.

On April 30, 1965, lot 25, 3.2 ha., was treated with Polystream-sand.

Effect on gastropods.—The divers made no observations. The treatment killed 89 percent of the oyster drills (100 percent of the thick-lipped drills and 46.6 percent of the Atlantic oyster drills) and reduced their numbers from 4.2 to 0.5 per square meter (table 4).

Effect on associated animals.—The divers made no observations.

Effect on predation.—Lot 25 was planted with small oysters in 1965, 1966, and 1967. Each year oysters were grown on the bed during their first summer of life and then transplanted to another bed the following spring. When first planted in June, July, August, and early September, the oysters were about 5 to 10 mm. long. By late November most of them had grown to 40 to 60 mm.

Predation on the oysters was light in each of the 3 years. On October 1, 1965, examination of the bed showed that less than 5 percent of the oysters had been killed by oyster drills and starfish combined. On July 22, 1966, divers observed that no oysters had been drilled. By October 9, 1967, oyster drills and starfish had killed 4.3 percent of the oysters on one section of the lot and 8.1 percent on another section. Predation by starfish was responsible for most of the mortality.

Area 7: Norwalk Harbor, Conn., 1966

Norwalk Harbor is interspersed with several small islands that protect oyster beds in channels and bays from storms. Water over the beds is from 2 to 6 m. at low tide, and the strongest currents run about 3.5 km. per hour.

Lot 42 in Norwalk Harbor was treated with Polystream (Granular) on August 24, 1966. Depth of water at mean low tide averages about 3 m.; maximum current is 3.5 km. per hour. Divers reported that strong currents carried off the lot a portion of the granules.

Effect on gastropods.—Before the treatment, divers counted up to five oyster drills of both species on each cluster of oysters. Within an hour after the treatment all visible thick-lipped drills and Atlantic oyster drills on clusters of oysters were swelling.

On September 8, 1966, 14 days after the treatment, divers observed that most oyster drills attached to clusters of oysters had fallen to the bottom. In a few instances, however, one or two oyster drills that were protected by being attached on the underside of clusters were unaffected and some were feeding on oysters.

On frequent inspections of the lot divers found that most oyster drills remained stunned, in a semiswollen condition, until November. A small number of drills may have recovered before the water dropped below 10° C., the temperature at which they normally become dormant.

As far as divers could determine, the treatment of lot 42 on August 24 did not kill many oyster drills but only immobilized them and prevented them from feeding. I suspected that a higher percentage would have been killed if the treatment with Polystream had been made in late April or early May.

To determine more precisely the effect of Polystream in the summer, however, an oyster company

treated lot 205, in a more protected area. Tidal currents over this lot run at no more than 0.9 km. per hour and, therefore, did not carry off the Polystream (Granular). The water is about 2 m. deep at low tide. On September 15, when the lot was treated, the water temperature was about 21° C.

A month later determinations with the hydraulic sampler showed that the treatment killed 78 percent of the oyster drills (no separation of species was made) (table 4).

Effect on associated animals.—On lot 42, divers reported that a large number of pipefish, juvenile flounders, mud crabs, and shrimp were stunned by the chemical an hour after the treatment, but these animals appeared to be normal later. They made no observations on lot 205.

Effect on predation.—In early May 1966, lot 42 was planted with 350 hl. of 1-year-old oysters (5,000–6,000 individuals per bushel). On June 17, 7 weeks later, oyster drills had killed 4.3 percent of the oysters and had reduced the number of live oysters per cluster from 19 to 18.2.

By July 25, 12 weeks after the planting, the rate of kill by oyster drills had increased tremendously. For example, 34 percent of the oysters had been killed around the edges of the bed and 26 percent in the center. Thus, during the period of 5 weeks, from June 17 to July 25, the average kill was 4.8 oysters per cluster, or nearly one oyster per cluster per week.

On August 24, the day the lot was treated, a third sampling was made. In areas around the edges of the lot, where oysters were planted thinly, clusters averaged only two live oysters each. In the center of the lot the number of live oysters per cluster averaged between 9 and 10. Thus, even in the main portions of the lot about 50 percent of the oysters had been destroyed. Oyster drills caused almost all the mortality; starfish caused only a small amount.

The fourth sampling was made on September 8. In the main portion of the lot, clusters had an average of ten 1-year-old oysters and, in addition, 18.3 live spat had attached to each cluster. By counting small oyster scars I determined that the original 1966 oyster set had averaged about 30 per cluster. Thus, even in the center of the lot, oyster drills had destroyed more than a third of the 1966 oyster spat by the time of treatment, August 24.

By observing these oysters through the fall of 1966 and into the spring of 1967, I found that virtually no additional oysters were killed by oyster drills. On March 31, 1967, clusters in the main portion of the lot averaged 9.3 2-year-olds (in 1966 they were 1-year-olds) and 21.5 1-year-olds of the 1966 oyster set. No careful determinations were made on lot 205. Later periodic observations indicated, however, that predation by oyster drills was slight.

In the spring of 1967, when these oysters were transplanted to another lot, their volume had increased to 2,100 hl., a sixfold increase during one growing season. I did not determine the increase in size of individual oysters.

Area 8: Norwalk Harbor, Conn., 1967

Five lots in Norwalk were treated with Polystream (Granular) between April 29 and May 13, 1967. Lot 42 was treated again and two lots alongside, lots 40 and 50, were treated for the first time. Depths of water and current velocities are about the same over these three lots. Lots 18 and 49 were also treated for the first time. The depth of water over these lots at low tide is about 2.5 m. and current velocities do not exceed 0.9 km. per hour. Lot 19, adjacent to lot 18, was not treated and served as a control.

Effect on gastropods.—Divers made no observations during or immediately after these treatments.

On lot 18 the treatment killed 52 percent of the oyster drills (68 percent of the thick-lipped drills and apparently none of the Atlantic oyster drills—again, numbers of Atlantic oyster drills were too low for significant comparisons) and reduced their numbers from 8.4 to 4.0 per square meter (table 4).

On lot 40 the treatment killed 78 percent of the oyster drills (82.2 percent of the thick-lipped drills and apparently 66.7 percent of the Atlantic oyster drills—again, numbers of the latter species were too low for accurate appraisal) and reduced their numbers from 16.7 to 3.8 per square meter (table 4).

On lot 42 the treatment killed 44 percent of the oyster drills (66.7 percent of the thick-lipped drills and apparently no Atlantic oyster drills—numbers of Atlantic oyster drills were too low for reliable comparisons) and reduced their numbers from 3.3 to 1.9 per square meter (table 4). Because most

oyster drills were killed on this lot by the second treatment and not by the first in 1966, I believe that treatments in early May are much more effective than those made later in the summer.

On lot 49 the treatment killed 86 percent of the oyster drills (84.6 percent of the thick-lipped drills and apparently all of the Atlantic oyster drills) and reduced their numbers from 6.3 to 0.9 per square meter (table 4).

On lot 50 the treatment killed 84 percent of the oyster drills (86.4 percent of the thick-lipped drills and 55.6 percent of the Atlantic oyster drills) and reduced their numbers from 13.9 to 2.3 per square meter (table 4).

Lot 19, which served as a control, was sampled at the same time as the other lots. The density of oyster drills per square meter was about the same on each date; on May 10 it was 19.5, and on June 30 it was 21.2 (table 4).

Effect on associated animals.—Divers did not examine these lots closely during or immediately after treatment. At intervals during the summer of 1967, however, they observed that healthy flounders, young starfish, mud crabs, and other animals were numerous on the beds. They saw no affected animals. In fact, most animals were more numerous on treated lots than on areas barren of oysters nearby. The divers did not count the young starfish on unplanted areas, but on October 6 they counted 8.8 young-of-year starfish per square meter on lot 18, and 35.3 per square meter on lot 40.

Effect on predation.—I carefully recorded mortalities of oysters on these lots from the time they were planted through November when oyster drills became dormant. In May 1967, 1- and 2-year-old oysters were planted on lot 40 and 1-year-old oysters were planted on lots 42, 49, and 50; and from June through early September, 1967-year-class hatchery-reared seed oysters about 5 mm. in length were planted on lot 18. Losses of oysters because of predation by oyster drills did not exceed 1.5 percent on any of these lots by late November (table 5). Because enough drills were present on some lots to cause higher mortalities—lot 40, for instance, had 3.8 oyster drills per square meter, and lot 50 had 2.3 per square meter—most live oyster drills must have been sufficiently "stunned" by the Polystream to prevent their feeding. This apparent "stunning" effect was also evident on lot 42 in 1966.

Oysters planted on these lots freshly treated with Polystream grew normally. For example, the 1-year-old oysters on lot 50 increased in volume from an average of less than 1 cc. to about 15 cc. each during the 1967 growing season. My determinations of growth of oysters planted on untreated bottoms show that this amount of growth is about normal.

Area 9: Foster's Cove, R.I., 1967

Foster's Cove on the south shore of Rhode Island, about 4 ha. in area, is a tidal pond connected to Charlestown Pond by a narrow inlet. Depth of water over the oysters ranges from 0 to 2 m. at low tide. There is little exchange of water between the two areas; thus, the principal water currents in the cove are caused by winds. Examination of three sections of Foster's Cove on November 10, 1966, indicated that oyster drills had killed about 75 percent of the oysters.

On May 31, 1967, two areas totaling 0.8 hectare were treated with Polystream (Granular).

Effect on gastropods.—Divers made no observations during or immediately after treatment. My later observations showed that the treatment killed all Atlantic oyster drills (no thick-lipped drills were present) in both areas and reduced their numbers from 9.5 and 3.6 to 0.0 per square meter (table 4).

Effect on associated animals.—On June 8, 8 days after the treatment, I examined the areas by walking along the shores and divers also examined them. Along the north shore, perhaps 15 m. from one of the treated areas, there were 4 dead toadfish, *Opsanus tau;* 50 dead silversides, *Menidia menidia;* 500 to 1,000 dead mummichogs; 4 dead blue crabs, *Callinectes sapidus;* 50 dead shrimp;

TABLE 5.—*Percentage of oysters killed by oyster drills and starfish in center areas of lots in Norwalk, Conn., 1967*

[Accumulated monthly totals [1]]

Lot number	May	June	July	Aug.	Sept.	Oct.	Nov.
				Percent			
18 [2]	0.0	0.0	0.0	0.6	0.4	1.0	0.2
40 [4]	.0	.0	0.0	1.0	0.0	0.0	.5
42 [3]	.0	.0	0.9	0.5	1.0	0.0	.5
49 [3]	.0	.0	0.0	0.0	0.3	1.5	.0
50 [3]	.0	.2	1.0	0.0	1.0	0.7	.0

[1] Sampling errors account for slight variation in numbers.
[2] Oysters raised in hatcheries in 1967.
[3] 1-year-old oysters.
[4] Mixture of 1965 and 1966 oyster set (1 and 2 years old).

and 10 dead polychaetes. On the inspections made along the shoreline, just inside the other treated section, there were only two dead toadfish and one dead blue crab. Undoubtedly, a high percentage of fish, blue crabs, and shrimp was killed at the time of treatment. Divers did not see any fish or shrimp, live or dead, either on or off treated areas.

Effect on predation.—No determinations were made.

Area 10: Fresh (Quahog) Pond, Falmouth, Mass., 1967

Fresh Pond, about 2.0 ha., is a tidal pond on the east shore of Buzzard's Bay. It is connected with the Bay by a long, narrow creek only about 1 m. wide and 0.3 m. deep at the entrance of the pond. The area for growing oysters is from 0 to 2 m. deep. Winds generate the principal currents in the pond.

On May 29, 1967, a 0.08-ha. section of the pond was treated with Polystream (Granular).

Effect on gastropods.—Within an hour of the treatment divers observed that all snails were beginning to swell.

By July 11, the treatment had killed 95 percent of the Atlantic oyster drills (no thick-lipped drills were present) and reduced their numbers from 40.8 to 2.2 per square meter (table 4).

An untreated area in another section of the pond that served as a control for the treatment had an average on May 29 of 37.2 Atlantic oyster drills per square meter. On July 11 this control plot had 33.2 drills per square meter.

Effect on associated animals.—Because the treatment extended to the shoreline of the pond, a number of observations could be made by walking along the shore. An hour after the treatment I observed 2 flounders (5 cm. long), 5 green crabs, *Carcinus maenas*, and 200 shrimp all dying, and 100 mummichogs stunned. I also observed three small schools of silversides swimming through the area; all these fish were healthy. New England nassas and mud snails, *Nassarius obsoletus*, were beginning to swell.

On July 11, 1967, divers examined the area again. The only animal affected other than snails was a tautog which weighed about 1.8 kg. All New England nassas and mud snails were dead.

Effect on predation.—The area had no oysters.

RECOMMENDATIONS FOR USING POLYSTREAM

During this study I made a number of observations on the use of Polystream (Granular), the form now most commonly used on commercial oyster beds to control oyster drills. These observations are listed below and should be emphasized for those who might wish to use this product:

1. The bed to receive a treatment should have a firm bottom, free of silt.
2. Treatments should be made in late April or early May when oyster drills first become active after a period of winter dormancy.
3. Polystream (Granular) should be spread at slack current.
4. Most successful treatments have been made in water less than 6 m. deep, where currents are less than 2.7 km. per hour. Where currents are stronger than this, planted oysters appear to prevent the Polystream (Granular) from being carried off a bed.
5. Polystream (Granular) treatments are successful on beds planted with seed oysters.
6. In certain shallow areas, where little or no current flows, a smaller quantity of Polystream (Granular) may be successful.

SUMMARY

1. Five experimental and 10 commercial treatments of oyster beds were made with Polystream in the States of Connecticut, New York, Rhode Island, and Massachusetts.

2. Immediately after a treatment, oysters, clams, and other organisms accumulated small residues of Polystream in their tissues. These residues, however, were gradually lost or greatly diminished. For instance, oysters and clams lost the residue of Polystream within 119 days. If they were transplanted from a treated to an untreated bed, however, they lost the residue within a week.

3. All oyster drills were killed in areas where water current velocities were low. On a typical bed, in an area where current velocities were between 0.9 and 2.7 km. per hour, however, about 85 percent of thick-lipped drills and 66 percent of Atlantic oyster drills were killed. Apparently, no oyster drills were killed where current velocities were strong.

4. On treated beds where current velocities were low, significant percentages of fish, small clams,

and other invertebrates were killed. On treated beds where current velocities were between 0.9 and 2.7 km. per hour, treatments killed only small percentages of fish, small clams, crabs, and other invertebrates. A few hours after the treatment the area appeared to be nontoxic to these animals.

5. A higher percentage of oyster drills was killed by treatments made in late April and early May than later in the summer.

6. Oyster drills were killed by the toxic action of Polystream, not by fish or crabs after they became swollen. In a small number of instances, however, they were consumed by starfish.

7. Oyster drills that survived a treatment appeared to be affected by the treatment to the extent that they did not feed significantly for a few months and, thus, did not kill many oysters.

8. The number of oyster drills on a bed where seed oysters were planted and removed each year remained low for at least 2 years.

9. Oyster drills killed less than 2 percent of young oysters during the first year on most treated beds.

10. Growth of oysters appeared to be normal on treated beds. For example, on one bed 1-year-old oysters increased in volume from less than 1 cc. to 15 cc. in one growing season.

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COMPARATIVE DISTRIBUTION OF MOLLUSKS IN DREDGED AND UNDREDGED PORTIONS OF AN ESTUARY, WITH A SYSTEMATIC LIST OF SPECIES[1]

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ABSTRACT

A survey of benthic mollusks in Boca Ciega Bay, Fla., showed a much smaller number and variety of species in the soft sediments in dredged canals than in the predominantly sand and shell sediments in undredged areas. Samples contained an average of 60.5 live mollusks and 3.8 species in undredged areas and 1.1 individuals and 0.6 species in dredged canals. A list of mollusks collected in this survey and in past studies is appended.

This report compares the numbers and varieties of mollusks in fine sediments of dredged canals with those found in undisturbed bottoms of sand and shell in Boca Ciega Bay, Fla. The bay is a shallow coastal lagoon of about 70 km.[2] which connects with Tampa Bay at its southern end (fig. 1). Some of the previous investigations in the lagoon included studies of sediments (Goodell and Gorsline, 1961; Taylor and Saloman, 1969); hydrology (Saloman and Taylor, 1968); submerged vegetation (Pomeroy, 1960; Phillips, 1960); fishes (Springer and Woodburn, 1960; Sykes and Finucane, 1964); and benthic invertebrates (Hutton, Eldred, Woodburn, and Ingle, 1956; Bullock and Boss [2]).

A recent evaluation of the effects of dredging and filling has documented a large loss of estuarine resources in Boca Ciega Bay (Taylor and Saloman, 1968). It was here that scientists and conservationists were finally successful in suppressing a dredge-fill proposal of 202 ha. (Sykes, 1967). This is also the bay in which the U.S. Army Corps of Engineers denied a dredge-fill application for the first time on the basis of fish and wildlife values, thus providing a stimulus for more comprehensive assessments of the biological and recreational aspects involved in future bayfill developments.

Thorson (1956) and others have concluded that sediment composition is a cardinal factor in controlling the settlement and viability of many marine invertebrates. The distribution of sessile benthic mollusks indicates to the marine ecologist the ability of the environment to support life. Marked deficiencies in abundance and variety indicate abnormality of the environment, and the degree of deficiency is roughly proportional to the degree of abnormality.

PROCEDURES

Between September 1963 and August 1964, we took 107 bottom samples at 31 stations in Boca Ciega Bay (figs. 1 and 2). Seven stations were in canals between finger fills (1–7), and the other 24 (8–31) were in relatively undisturbed areas of the bay. We collected algae, sea grasses, and benthic animals with a bucket dredge and bottom drag (Taylor, 1965). In water less than 1 m. deep, three shovelfuls of bay bottom (about 15 l.) were substituted for the dredge haul. One station sample consisted of the combined catch from one bucket dredge (or three shovelfuls) and one bottom drag. At each station a subsample of sediment was taken from the dredge or shovel and was later analyzed at Florida State University.

[1] Contribution No. 57, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla. 33706.

[2] Bullock, R., and C. Boss. 1963. Ecological distribution of marine mollusks in Boca Ciega Bay, Florida. Winter term project. Mimeographed report on file at Florida Presbyterian College, St. Petersburg, Fla. 33733.

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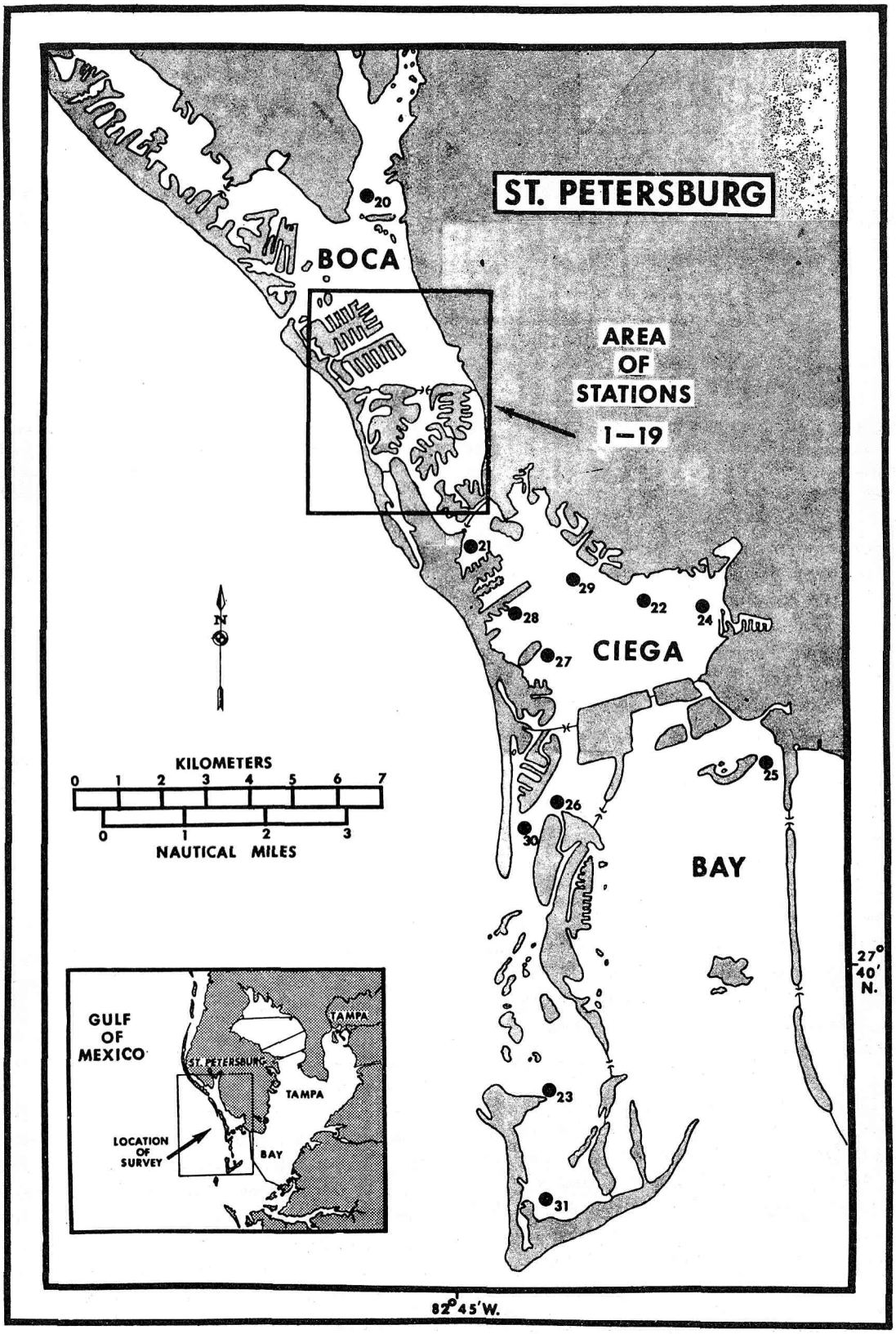

FIGURE 1.—Collecting stations 20 to 31 and area of stations 1 to 19 (see fig. 2), Boca Ciega Bay, Fla.

FIGURE 2.—Collecting stations 1 to 19, Boca Ciega Bay, Fla., between Johns Pass and Corey Causeway.

We washed samples for benthic organisms on a 24-mesh sieve which had an opening of 0.701 mm. and fixed the material retained by the sieve in a 10 percent sea-water Formalin [3] mixture. A protein stain (rose bengal) was added to facilitate the separation of small organisms from debris. Identified animals were preserved in 70 percent isopropanol.

We identified 168 species of mollusks representing 69 families; of these, representatives of 156 species were collected live. We based determinations on standard taxonomic works (Clench, 1941–69; McLean, 1951; Olsson, Harbison, Fargo, and Pilsbry, 1953; Abbott, 1954, 1968; Perry and Schwengel, 1955; Warmke and Abbott, 1962; Keen, 1963; Wagner and Abbott, 1967; an unpublished report by Bullock and Boss (see footnote 2), and collections at the University of

[3] Trade names referred to in this publication do not imply endorsement of commercial products.

South Florida [4] and the U.S. National Museum. Specimens from this study were deposited in the invertebrate reference collection of the BCF (Bureau of Commercial Fisheries) Biological Laboratory, St. Petersburg Beach, Fla.

MOLLUSK-SEDIMENT RELATIONS

Comparison of mollusks and bottom types showed that species and individuals were much less numerous in soft sediments of canals than in sandy sediments in undredged areas of Boca Ciega Bay (tables 1 and 2). Canal sediments, which averaged 85 percent silt and clay, had 16 live mollusks in 14 samples. Living specimens collected at the seven canal stations were the gastropods *Nassarius vibex* and *Haminoea antillarum*, and the pelecypods *Brachidontes exustus*, *Anomalocardia cuneimeris*, and *Mercenaria campechiensis*. These species and 151 others were collected live from the 24 stations in undredged areas of the bay. Sediments from natural bottom, which averaged 91 percent sand and shell, yielded 5,631 live mollusks in 93 samples.

Pratt (1953) suggested that soft sediments and associated hydrological conditions may be limiting because (1) rapid deposition has a smothering effect, (2) high organic content of soft sediments depletes dissolved oxygen, and (3) weak currents in areas of deposition are insufficient for the removal of toxic metabolic wastes. Comparisons of sediments and environmental factors (Taylor and Saloman, 1968) in dredged and undredged areas at sampling stations lead us to conclude that the soft sediment is the principal factor limiting the abundance and diversity of benthic mollusks in bayfill canals of Boca Ciega Bay. Such sediments are as thick as 4 m. in waterways that were dredged 15 years ago.

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[4] Hillman Collection, University of South Florida, Tampa, Fla. 33620.

TABLE 1.—*Depth, bottom type, and number of live mollusks collected at stations in dredged canals in Boca Ciega Bay, Fla., 1963–64*

Canal station	Depth	Bottom type		Species per sample	Individual per sample
		Sand size and larger	Silt and clay		
	M.	*Percent*	*Percent*	*Number*	*Number*
1	4	6	94	1.0	1.0
2	3	7	93	1.0	1.5
3	4	5	95	0	0
4	3	60	40	1.0	2.0
5	6	7	93	0	0
6	4	6	94	.5	1.0
7	4	14	86	.5	2.5
Average	4	15	85	.6	1.1

TABLE 2.—*Depth, bottom type, and number of live mollusks collected at stations in undredged areas of Boca Ciega Bay, Fla., 1963–64*

Stations in undredged areas	Depth	Bottom type		Species per sample	Individual per sample
		Sand size and larger	Silt and clay		
	M.	*Percent*	*Percent*	*Number*	*Number*
8	2.5	98	2	3.5	8.0
9	1.0	99	1	3.0	7.3
10	.5	89	11	.5	.5
11	1.5	97	3	4.0	25.0
12	.5	96	4	.5	2.5
13	2.0	96	4	3.5	18.0
14	1.7	88	12	.5	2.0
15	.5	92	8	2.6	20.6
16	.7	99	1	.3	.7
17	5.0	83	17	1.0	2.5
18	1.5	96	4	6.5	58.0
19	1.0	84	16	1.6	24.0
20	.5	99	1	5.6	140.0
21	1.0	98	2	3.4	67.8
22	2.0	98	2	2.8	71.8
23	7.0	98	2	4.3	66.6
24	2.0	79	19	11.7	316.0
25	.7	97	3	3.2	8.4
26	7.0	99	1	4.0	16.7
27	.7	97	3	5.0	11.0
28	3.0	12	88	4.7	56.3
29	2.0	87	12	6.7	89.0
30	.3	98	2	6.2	78.0
31	2.0	95	5	4.0	86.5
Average	1.9	91	9	3.8	60.5

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APPENDIX

A Checklist Of Mollusks From Boca Ciega Bay, Florida

We identified 168 species of mollusks representing 69 families from BCF collections in Boca Ciega Bay. Of these, members of 156 species were alive. The number was increased to 72 families and 188 species by including mollusks recorded in other studies. The additions are coded within the list by surname initials of the authors who reported them: B. and B.—Bullock and Boss (see footnote 2); H.—Hutton et al. (1956); D. and K.—Dragovich and Kelly (1964). Mollusks not collected alive in this investigation are denoted by an asterisk (*). We identified some specimens only after comparison with specimens in the U.S. National Museum (+). Classifications are based on Abbott (1954, 1968) and Warmke and Abbott (1962).

CLASS GASTROPODA

Fissurellidae

Diodora cayenensis (Lamarck)

Trochidae

**Calliostoma jujubinum tampaense* (Conrad)

Turbinidae

Arene tricarinata (Stearns)
Turbo castaneus (Gmelin)

Neritidae

**Neritina reclivata* (Say)

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Melanellidae

Melanella bilineata (Alder)
Melanella intermedia (Cantraine)

Epitoniidae

Epitonium angulatum (Say)
Epitonium humpreysi (Kiener)
Epitonium rupicola (Kurtz)

Rissoidae

Rissoina chesneli (Michaud)

Vitrinellidae

Cyclostremiscus beaui Fisher—further verification pending.
Cyclostremiscus suppressus Dall—futher verification pending.
+*Teinostoma cryptospira* (no author on specimen)—further verification pending.

Truncatellidae

**Truncatella pulchella* Pfeiffer

Turritellidae

Vermicularia fargoi Olsson

Caecidae

Caecum cooperi S. Smith
Caecum pulchellum Stimpson
Meioceras nitidum (Stimpson)

Modulidae

Modulus modulus (Linné)

Cerithiidae

Bittium varium (Pfeiffer)
Cerithiopsis emersoni (C. B. Adams)—B. and B.
Cerithiopsis greeni (C. B. Adams)
Cerithium muscarum Say
Cerithium floridanum Mörch
Seila adamsi (H. C. Lea)

Triphoridae

Triphora nigrocincta (C. B. Adams)

Potamididae

Batillaria minima (Gmelin)

Calyptraeidae

Calyptraea centralis Conrad
Crepidula aculeata (Gmelin)
Crepidula fornicata (Linné)
Crepidula maculosa Conrad
Crepidula plana Say

Strombidae

Strombus alatus Gmelin—B. and B.

Naticidae

Natica pusilla Say
Polinices duplicatus (Say)
Sinum perspectivum (Say)—B. and B.

Muricidae

Eupleura sulcidentata Dall
Murex cellulosus Conrad
Murex pomum Gmelin
Thais haemastoma floridana (Conrad)—B. and B.
Urosalpinx perrugata (Conrad)

Buccinidae

Busycon contrarium (Conrad)
Busycon spiratum (Lamarck)

Columbellidae

+*Anachis semiplicata* Stearns
Anachis obesa (C. B. Adams)
Anachis ostreicola Sowerby
Columbella rusticoides Heilprin—B. and B.
Mitrella lunata (Say)

Melongenidae

Melongena corona (Gmelin)

Nassariidae

Nassarius vibex (Say)

Fasciolariidae

Fasciolaria hunteria (Perry)
Fasciolaria tulipa (Linné)
Pleuroploca gigantea (Kiener)—H.

Olividae

Oliva sayana Ravenel
Olivella perplexa Olsson
Olivella mutica (Say)
Olivella floralia Duclos

Marginellidae

Bullata ovuliformis (Orbigny)
Hyalina avenacea (Deshayes)
Marginella aureocincta Stearns
Persicula lavalleeana (Orbigny)
Prunum apicinum (Menke)

Conidae

Conus floridanus Gabb—H.
Conus jaspideus Gmelin—H.
**Conus stearnsi* Conrad

Terebridae

Terebra concava vinosa Dall
Terebra dislocata Say
Terebra protexta Conrad

Turridae

**Glyphoturris rugirima* (Dall)
**Monilispira leucocyma* (Dall)
Pyrgocythara hemphilli Bartsch and Rehder
Stellatoma stellata (Stearns)

Bullidae

Bulla striata Bruguière

Atyidae

Haminoea antillarum (Orbigny)
Haminoea succinea (Conrad)

Retusidae

Retusa canaliculata (Say)

Pyramidellidae

Odostomia acutidens Dall
Odostomia impressa (Say)
Odostomia producta Dall
Odostomia seminuda C. B. Adams
Odostomia sp.
Pyramidella crenulata (Holmes)
+*Sayella hemphilli* (Dall)
Turbonilla conradi Bush (Dall)
Turbonilla dalli Bush

Acteocinidae

Cylichna bidentata (Orbigny)

Acteonidae

Acteon punctostriatus (C. B. Adams)

Aplysiidae

Bursatella leachi plei Rang

Ellobiidae

Melampus coffeus (Linné)

CLASS AMPHINEURA

Ischnochitonidae

Chaetopleura apiculata (Say)
Ischnochiton papillosus (C. B. Adams)

Chitonidae

Chiton tuberculatus Linné—H.

CLASS SCAPHOPODA

Dentaliidae

Dentalium eboreum Conrad
Dentalium antillarum Orbigny
Dentalium sp. (resembles *D. texasianum* Philippi)

CLASS PELECYPODA

Solemyacidae

Solemya occidentalis Deshayes

Nuculidae

Nucula proxima Say

Nuculanidae

Nuculana acuta Conrad

Arcidae

Anadara transversa (Say)
**Arca zebra* Swainson
Barbatia cancellaria (Lamarck)
Barbatia candida (Helbling)—D. and K.
Noetia ponderosa (Say)

Glycymerididae

Glycymeris pectinata (Gmelin)

Pinnidae

Atrina rigida Lightfoot

Mytilidae

Amygdalum papyria (Conrad)
Brachidontes exustus (Linné)
Lioberus castaneus (Say)
Lithophaga bisulcata (Orbigny)
Modiolus demissus (Dillwyn)—H.
Modiolus demissus granosissimus (Sowerby)—B. and B.
Modiolus americanus (Leach)
Musculus lateralis (Say)

Plicatulidae

Plicatula gibbosa Lamarck

Ostreidae

Crassostrea virginica (Gmelin)
Ostrea equestris Say
Ostrea frons Linné

Pectinidae

Aequipecten irradians concentricus (Say)

Anomiidae

Anomia simplex Orbigny

Crassatellidae

Crassinella lunulata Conrad

Carditidae

Cardita floridana Conrad
Venericardia perplana (Conrad)
Venericardia tridentata (Say)

Corbiculidae

Pseudocyrena floridana (Conrad)—B. and B.

Erycinidae

Erycina floridana Vanatta
Mysella planulata (Stimpson)

Montacutidae

Montacuta floridana Dall

Lucinidae

**Anodontia alba* Link
Anodontia philippiana (Reeve)
Codakia orbiculata (Montagu)—B. and B.
Lucina multilineata (Tuomey and Holmes)
Phacoides nassula (Conrad)

Diplodontidae

Diplodonta punctata (Say)

Chamidae

**Chama congregata* Conrad

Cardiidae

Dinocardium robustum vanhyningi (Clench and L. C. Smith)
Laevicardium mortoni (Conrad)
Trachycardium egmontianum (Shuttleworth)
Trachycardium muricatum (Linné)

Veneridae

Anomalocardia cuneimeris (Conrad)
Chione cancellata (Linné)
Chione grus (Holmes)
Chione intapurpurea Conrad—B. and B.
Cyclinella tenuis (Recluz)
Dosinia discus (Reeve)
Dosinia elegans Conrad—B. and B.
Macrocallista nimbosa Lightfoot
Mercenaria campechiensis (Gmelin)
Parastarte triquetra (Conrad)
Pitar fulminata (Menke)
Pitar simpsoni (Dall)
**Transennella conradina* Dall
**Transenella stimpsoni* Dall

Petricolidae

Petricola pholadiformis Lamarck

Mactridae

Anatina plicatella (Lamarck)
Mactra fragilis Gmelin
Mulinia lateralis (Say)
Spisula solidissima (Dillwyn)—B. and B.

Tellindae

Psammotreta intastriata (Say)—B. and B.
Macoma constricta (Bruguière)
Tellidora cristata Recluz
Tellina aequistriata Say
Tellina alternata Say
Tellina lineata Turton
Tellina mera Say
Tellina tampaensis Conrad
Tellina sp. (resembles *T. texana* Dall)
Tellina versicolor DeKay

Semelidae

Abra aequalis (Say)
Cumingia tellinoides (Conrad)
Semele bellastriata (Conrad)
Semele proficua (Pulteney)
Semele purpurascens (Gmelin)

Donacidae

Donax variabilis Say

Sanguinolarildae

Tagelus divisus Spengler
Tagelus plebeius (Lightfoot)

Solenidae

Ensis minor Dall

Corbulidae

Corbula barrattiana C. B. Adams
Corbula caribaea Orbigny
Corbula contracta Say

Pholadidae

Cyrtopleura costata (Linné)
Martesia cuneiformis Say

Pandoridae

**Pandora trilineata* Say
Pandora bushiana Dall

Lyonsildae

Lyonsia hyalina floridana (Conrad)

Periplomatidae

Periploma sp.

EFFECT OF WATER VELOCITY ON THE FISH-GUIDING EFFICIENCY OF AN ELECTRICAL GUIDING SYSTEM

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ABSTRACT

The study was performed in 1962 in a diversion of the Yakima River near Prosser, Wash. Massive structures for regulating the water velocity, producing the desired electrical field, and collecting the guided fish were installed. Evaluation facilities consisted of rotary drum screens to divert all fish that escaped past the electrical field to an inclined-screen trap. The fish tested were wild, downstream-migrating fingerlings of chinook salmon, *Oncorhynchus tshawytscha;* coho salmon, *O. kisutch;* and rainbow or steelhead trout, *Salmo gairdneri.* The variables were three water velocities, three species, and four test periods.

Fish-guiding efficiency tended to decrease with increasing water velocity. The guiding efficiencies of the electrical system at water velocities of 0.2, 0.5, and 0.8 (m.p.s.) meter per second were, respectively, 84.2, 54.2, and 50.2 percent for chinook salmon; 82.4, 47.8, and 42.8 percent for coho salmon; and 69.9, 40.2, and 44.8 percent for rainbow or steelhead trout. The guiding efficiency achieved was, thus, highest with chinook salmon, intermediate with coho salmon, and generally lowest with rainbow or steelhead trout.

The use of electricity to guide juvenile salmon and trout migrating downstream may be feasible in certain environments where the water velocity does not exceed 0.3 m.p.s. but does not appear practical for use in most rivers and streams.

One of the major problems facing fishery agencies in the Pacific Northwest is that of providing an efficient and economically feasible method of guiding juvenile salmon and trout past areas potentially dangerous to fish. The need is particularly acute in river systems affected by high dams and large, deep storage reservoirs. Recent studies (Durkin, Park, and Raleigh, 1970) indicate that under certain conditions many juvenile migrants fail to pass through large reservoirs, implying that if natural runs are to be perpetuated, downstream migrants must be guided and collected at the head of a reservoir or in its tributaries.

Various methods of guiding fish, including the use of electricity (Holmes, 1948; Andrew, Kersey, and Johnson, 1955), louvers (Bates and Vinsonhaler, 1957), and of lights and air bubbles (Brett and Alderdice, 1958) have been tested with varying degrees of success. Mason and Duncan [1] described experiments using the electrical guiding principle in which they successfully diverted about 90 percent of the juvenile migrants. Their experiments, however, were in water velocities of less than 0.3 m.p.s. Because the physical conditions at the upstream end of large reservoirs may vary considerably, a guiding system for the collection of juvenile salmon must operate efficiently under a variety of flow conditions.

The purpose of the present study was to determine the effect of three water velocities—0.2, 0.5, and 0.8 m.p.s.—on the fish-guiding efficiency of an electrical guiding system operating under field conditions.

EXPERIMENTAL SITE

Requirements of the experimental site were: ample flows that could be controlled, readily available electric power, sufficient downstream migrants to carry out the tests, and a convenient system for assessing the total outmigration. A section of the Chandler Canal (fig. 1), a diversion of the Yakima River near Prosser, Wash., met these requirements.

The Chandler Canal is about 2.4 m. deep, 19.8 m.

[1] Mason, James E., and Rea E. Duncan, *Development* and appraisal of methods of diverting fingerling salmon with electricity at Lake Tapps. Bur. Commer. Fish., Biol. Lab., Seattle, Wash. Manuscript.

Published June 1970.

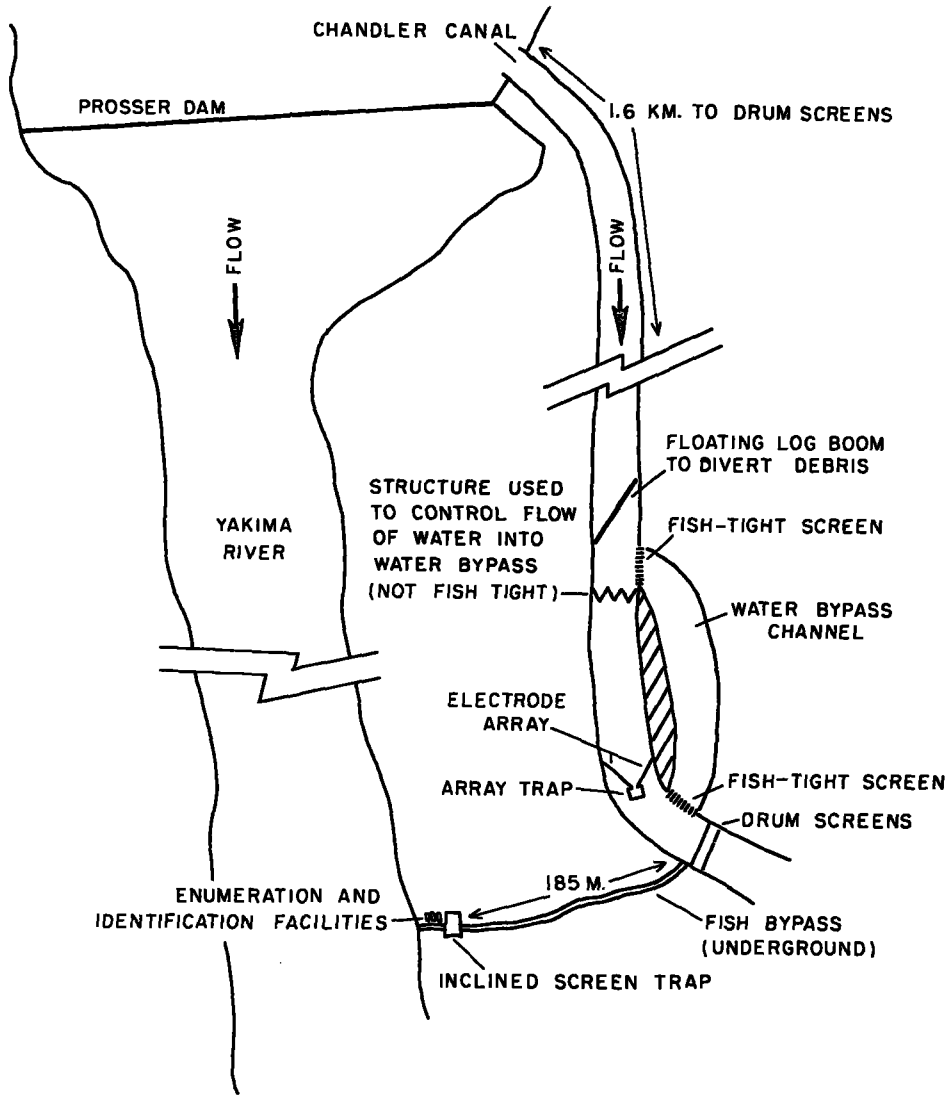

FIGURE 1.—Diagrammatic sketch of experimental site.

wide, and 14.5 km. long; it normally carries a flow of 28.3 to 34.0 c.m.s. (cubic meters per second). The banks have a 60° slope. The bottom consists primarily of sand and silt with some areas of small gravel. The water velocity is relatively uniform because large obstructions are lacking.

The entrance to the canal is not screened; juvenile fish migrating down the Yakima River have easy access, especially during periods of low water when a large portion of the river is diverted into the canal. To salvage these fish, the Bureau of Sport Fisheries and Wildlife operates rotary drum screens and a fish bypass system about 1.6 km. downstream from the canal intake. The experimental site consisted of a 439-m. section of the canal just upstream from the drum screens.

VELOCITY CONTROL STRUCTURES

Stoplogs, shunting panels, and screens were manipulated to effectuate and maintain the desired water velocities (0.2, 0.5, and 0.8 m.p.s.). Figure 2 is an aerial photo of the velocity control structures. A trash boom at the upstream end of the experimental site diverted floating debris to the bank where it was collected for disposal. Just downstream from the boom, flows could be diverted to the water-bypass channel (B, fig. 2),

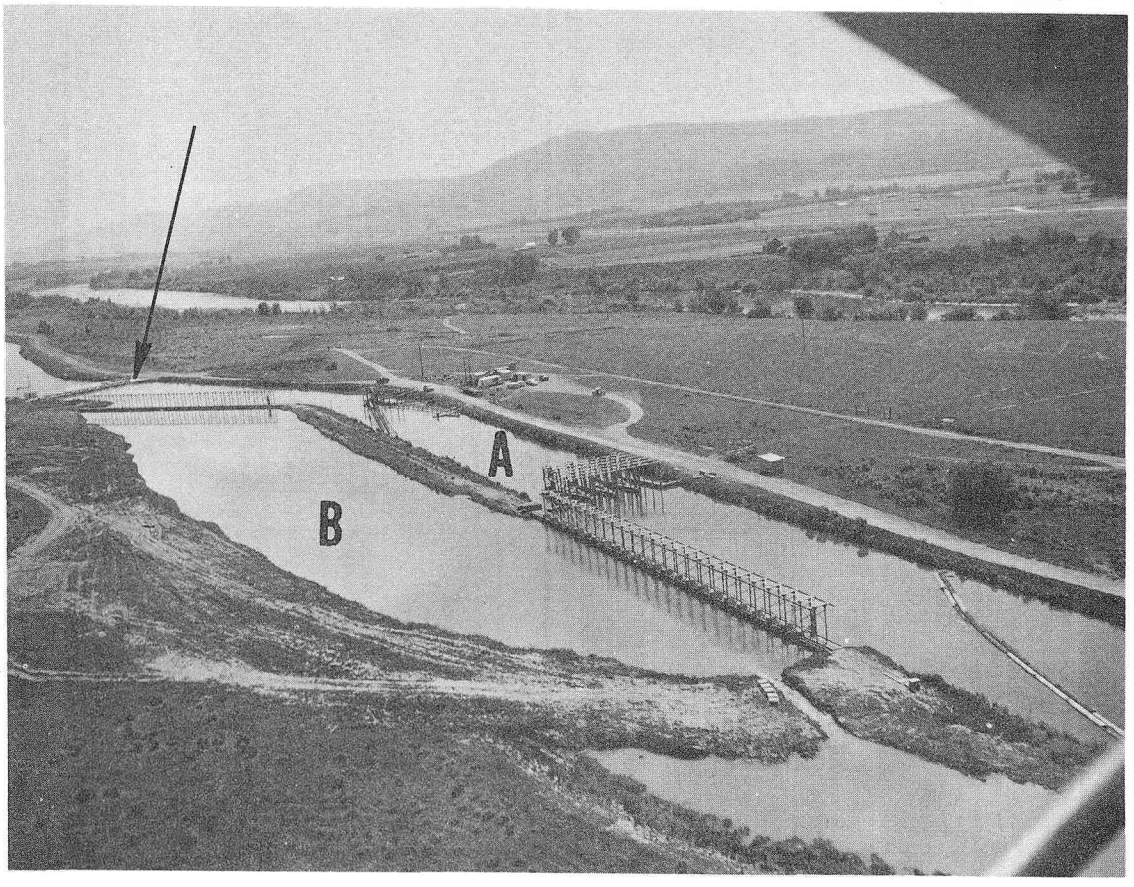

FIGURE 2.—Physical facilities of experimental fish-guiding site at Prosser, Wash. Waterflow is from right to left. Experimental canal (A) had V-type electrode array, an array trap, and a water-velocity control structure to divert excess flow through water-bypass channel (B). The water-bypass channel was screened at both ends to prevent entry of fish. Arrow points to rotary drum screens used to evaluate fish-guiding efficiency of electrical field created by electrode array. Yakima River is in background.

which was excavated adjacent and parallel to the Chandler Canal.

The bypass channel was about 1.2 m. deep, 288 m. long, and 64 m. wide. It carried the excess flow when reduced velocities were desired in the experimental canal. Both ends of this bypass channel were screened to prevent entry of fish (fig. 3). Each screen support structure consisted of a wooden framework, 72 m. long and 3 m. high, equipped with guides to accommodate 69 individual screens. Each screen was about 0.9 m. wide, 3 m. high, 3.2 mm. thick, and constructed of perforated steel plate. The perforations were 6.4 by 25.4 mm. ovals that provided a 46 percent opening. A traveling hoist on an overhead I-beam was used to lift the screens for cleaning. Each screen bay was fitted with a double set of guides so that a second screen could be installed before the first was removed.

The screen support structure at the entrance to the water-bypass channel was also equipped with guides to accommodate stoplogs. The stoplogs, constructed of concrete, were about 0.9 m. long, 0.6 m. high, and 5.1 cm. thick. An overhead hoist, similar to that used for lifting the screens, was used to raise and lower these stoplogs.

Another structure, at the upstream end of the main experimental canal and just downstream from the entrance to the water-bypass channel, was also used to help regulate the water velocity (fig. 4). This structure was constructed in the form of four V's joined together (VVVV) and was placed in the experimental canal at 90° to the flow. The structure was connected to each bank by earth-filled wooden abutments. The sides of each V were equipped with guides to accommodate 15 solid plywood panels. An overhead hoist raised or lowered

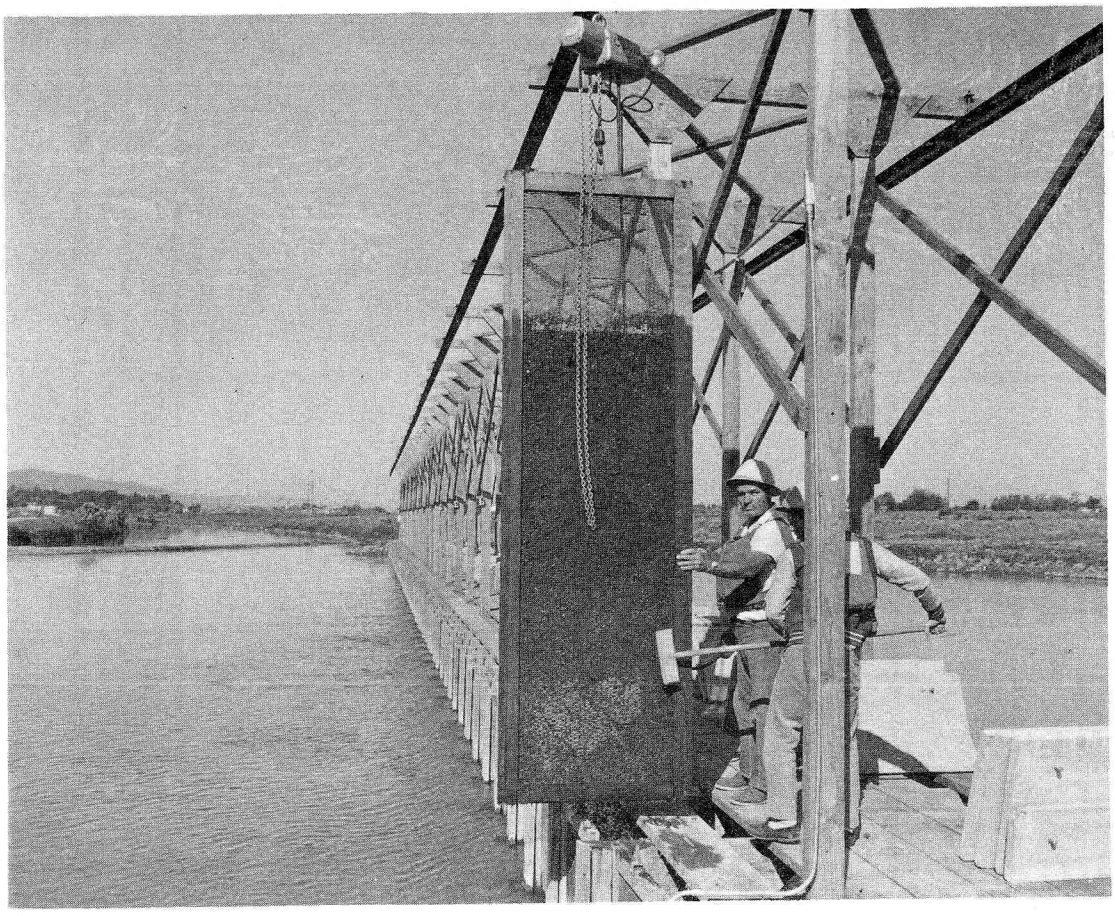

FIGURE 3.—Screen support and velocity control structure at entrance to water-bypass channel. Screen is raised for cleaning. Several concrete stoplogs are stacked in lower right foreground.

the panels. By installing various numbers of these plywood panels and adjusting the stoplogs in the velocity control structure at the entrance to the water-bypass channel, we could divert water to regulate the flow. At the slowest velocity tested—0.2 m.p.s.—the flow was about 7.4 c.m.s.; at 0.5 m.p.s. it was 22.2 c.m.s.; and at 0.8 m.p.s., 37.1 c.m.s. The three test velocities were average velocities and were maintained by routine cleaning of the screens. Actual water velocities varied about ±0.06 m.p.s. from the desired test velocities.

ELECTRODE ARRAY AND ELECTRICAL CONDITIONS

The angle of the electrode array to the water-flow and the electrical conditions of the array were held constant during the entire experiment. The array consisted of three rows of vertically suspended electrodes forming a 30° V (fig. 5). Because the electrode array trap was constructed nearer the right bank, looking downstream, and both legs of the array extended upstream at about a 15° angle to the flow, the legs were not exactly the same length. The left leg was 45.7 m. long, and the right leg 30.5 m. The electrodes were supported on the surface by a wooden framework and on the bottom by wooden dowels. One dowel extended from the bottom of each electrode and was driven into the sandy canal bottom about 10 cm. These dowels helped to keep the electrodes vertical at the higher water velocities and also insulated them from the canal bottom. The electrodes were 3-m. lengths of steel pipe with an outside diameter of 5.1 cm. The distance between the rows of electrodes in each leg of the array was 1.2 m. from the upstream row to the middle row and 0.6 m. from the middle to the downstream row. Spacing between the electrodes was 0.6 m. (fig. 6).

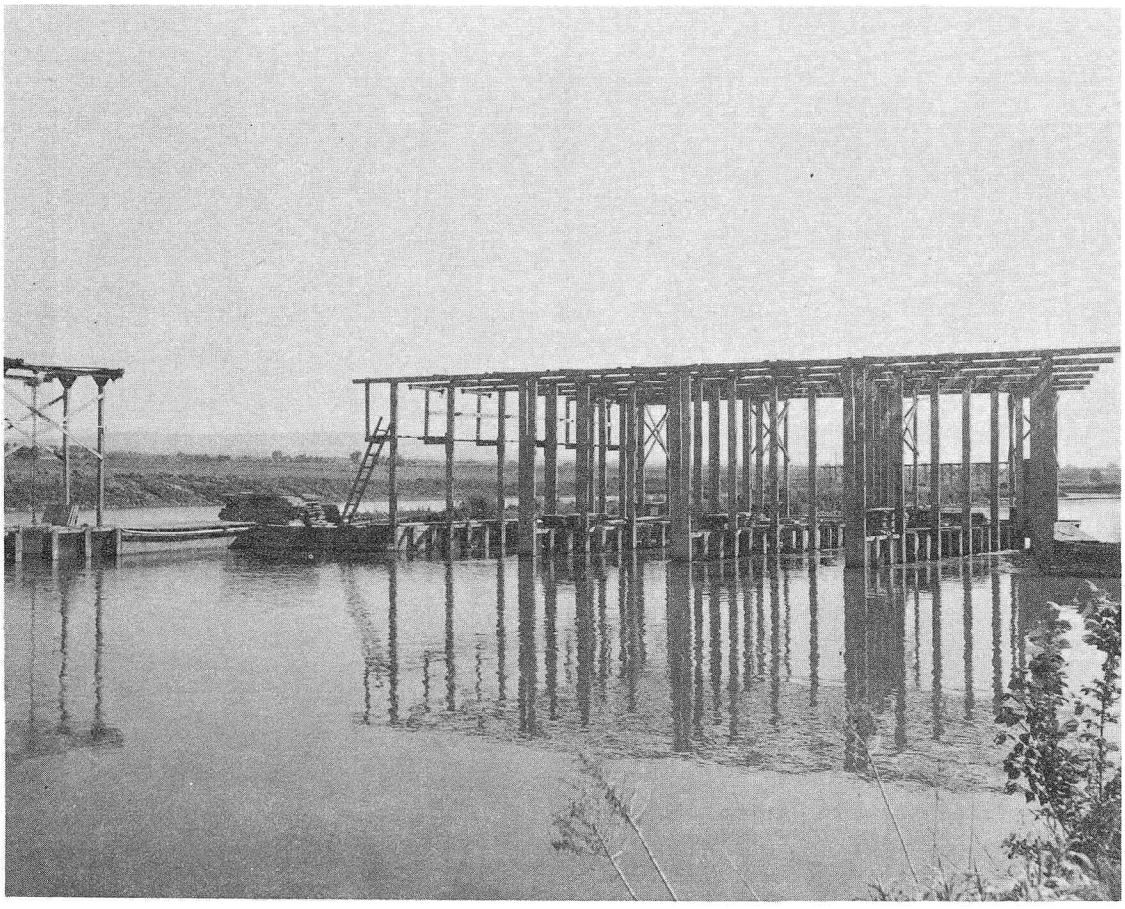

FIGURE 4.—Velocity control structure at upstream end of main experimental canal.

The electrodes were wired to make a total of five groups (fig. 7); when energized, each group produced an electrical field. The applied voltage to all of the electrodes was the same; hence, the voltage gradient created by the electrode arrangement and wiring pattern was higher on the downstream side than on the upstream side of the array. Figure 8 is an analog gradient plot of an electrical field created by one pulse at one specific location on the left side of the electrode array. The plotting interval is 10 percent of the applied voltage. Only one pulse of the five-pulse cycle is illustrated, but it is representative of the electrical fields produced with each pulse, because the wiring pattern was uniform with respect to electrode spacing.

The electrodes were energized with d.c., square-wave pulses, supplied by interrupting the output of a d.c. generator with sequential switching equipment (Volz, 1962). Figure 9 shows a block diagram of this equipment. The pulse amplitude was 125 volts, the duration 20 milliseconds, and the frequency 15 pulses per second. Because the electrodes were wired in five groups and the groups pulsed sequentially, each group was actually energized only three times per second (total pulse frequency divided by number of electrode groups). These electrical conditions had been tested in previous guiding experiments and had proved to be non-injurious to fish (Pugh, 1962).

Table 1 shows the pulsing sequence of the electrode array. When the first pulse was delivered, the electrodes connected to pulse supply cable 1 became positively energized and all the electrodes in the downstream row (pulse supply cable 6) became negatively energized. On the second pulse, the electrodes connected to pulse supply cable 2 became positively energized and the electrodes in the downstream row became negatively energized. This succession of pulses continued through pulse supply cables 3, 4, and 5. When the fifth pulse had been

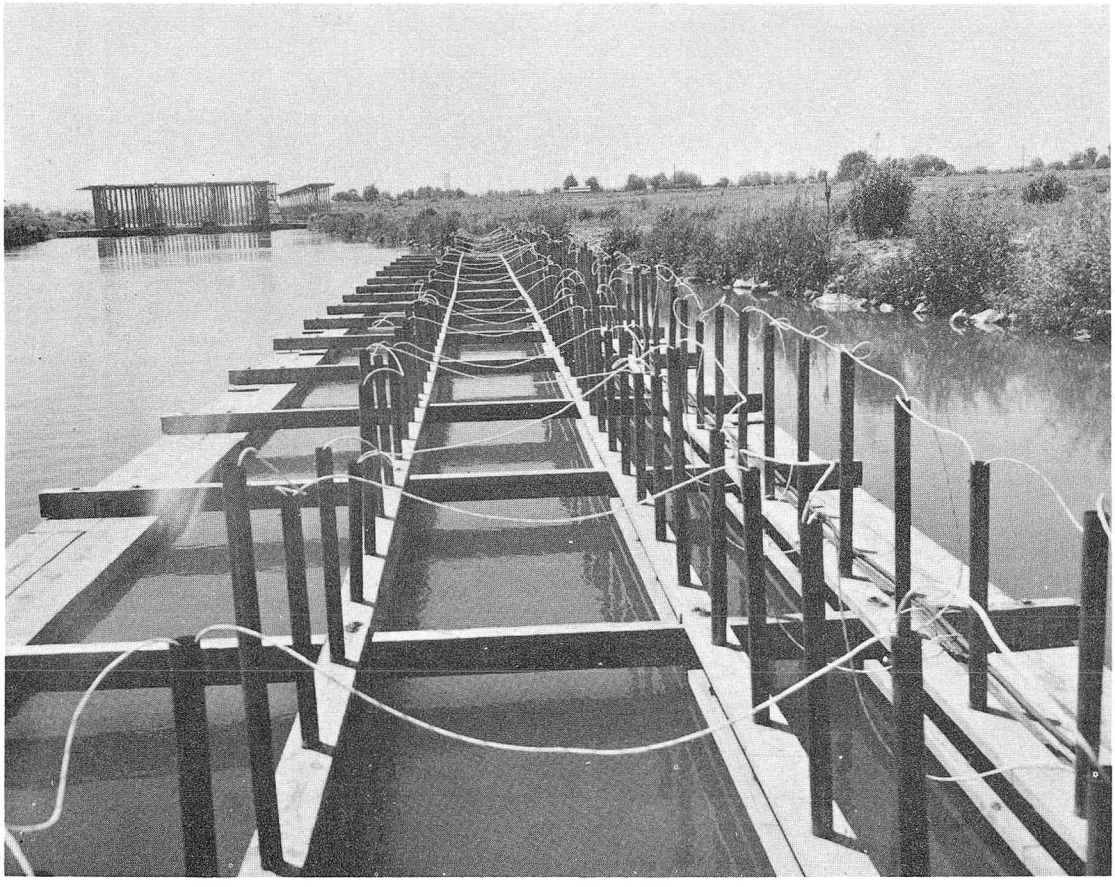

FIGURE 5.—One leg of electrode array.

delivered, the cycle was complete and the sequential pulsing equipment switched automatically to start the second cycle. During the second and each succeeding cycle, the electrodes were energized in exactly the same manner as they were during the first cycle.

Although the polarity of the electrodes was not alternated, we experienced very little electrolysis. Once the desired electrical conditions had been set into the sequential switching equipment, the gear functioned automatically and dependably for the duration of the experiment.

TABLE 1.—*Pulsing sequence and polarity of the electrode array*

Pulse supply-cable (number)	Pulsing sequence and polarity					
	Pulse 1	Pulse 2	Pulse 3	Pulse 4	Pulse 5	Pulse 1 (second cycle)
1	(+)	0	0	0	0	(+)
2	0	(+)	0	0	0	0
3	0	0	(+)	0	0	0
4	0	0	0	(+)	0	0
5	0	0	0	0	(+)	0
6	(−)	(−)	(−)	(−)	(−)	(−)

The purpose of a sequentially pulsed field, sweeping in the direction of the array trap, was to take advantage of any electrotactic effect that the electrical energy might produce. Although the electrode array and electrical conditions in this experiment were designed to divert the fish by stimulating an avoidance response at the periphery of the electrical field, it is known that when fish penetrate a pulsed d.c. electrical field of sufficient intensity they are stimulated to propel themselves in the direction of the positive pole or anode (Haskell, MacDougal, and Geduldig, 1954).

ARRAY TRAP

The array trap was at the downstream end of the electrode array. It was constructed with a 6.4 m.-wide entrance so that the effective electrical fields created by the converging legs of the elec-

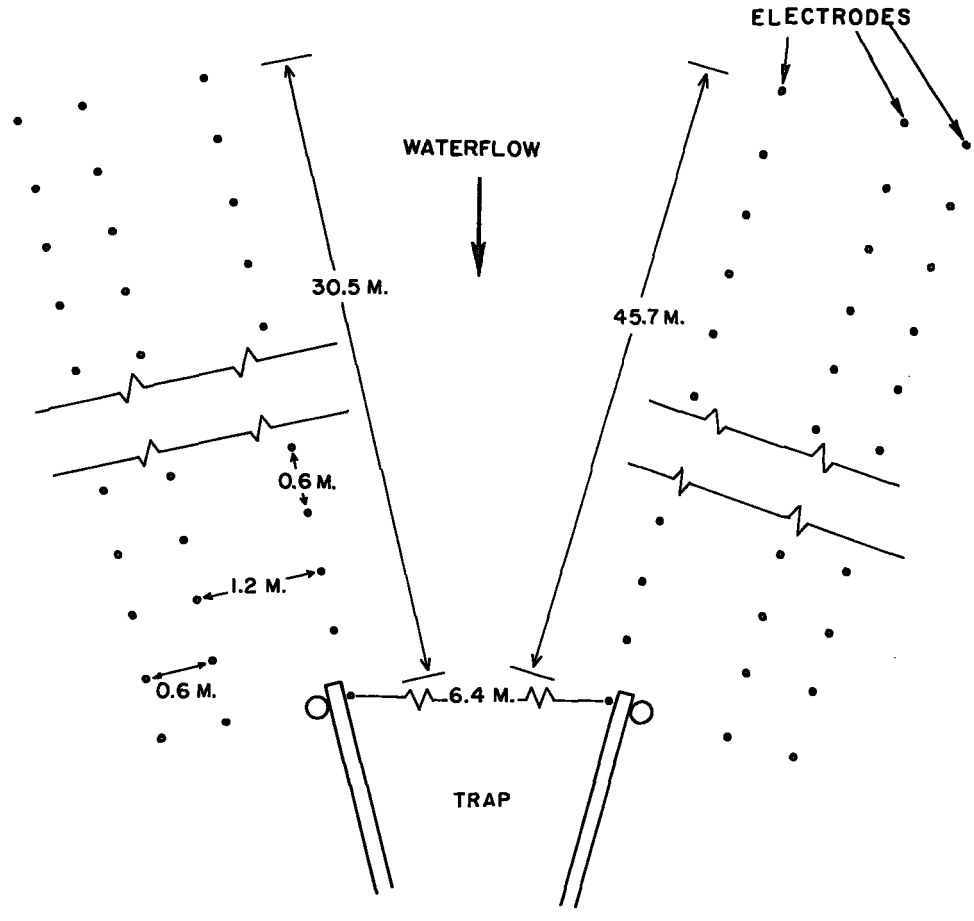

FIGURE 6.—Electrode array with spacing of electrodes as indicated.

trode array would not overlap and prevent the entry of fish. Observations indicated that the electrical field did not affect fish swimming more than 0.9 to 1.2 m. away from the electrodes; hence, any fish migrating in an area about 4.0 m. wide in the middle of the canal were able to enter the array trap without being visibly affected by the electrical energy.

The trap entrance occupied 34 percent of the cross-sectional area of the canal. Measurements showed that when the water velocity in the canal was 0.2 m.p.s., the trap screened about 33 percent of the flow. At higher water velocities the hydraulic head on the trap lead-in screens increased and some water tended to flow upstream around the end of the screens rather than through them. Consequently, the trap screened only about 29 percent of the flow at a water velocity of 0.5 m.p.s. and about 25 percent at 0.8 m.p.s.

The trap lead-ins, converging at a 30° angle (fig. 10) extended downstream from the trap entrance to the trap throat. Each of these lead-ins was 11.6 m. long and consisted of 11 screens of the same design and construction as those used in the velocity control structure at the entrance to the water-diversion channel. An overhead lifting device facilitated the cleaning of the screens. The trap throat was 0.5 m. wide by 2.4 m. deep. It was equipped with guides to accommodate a gate that could be closed when the trap was being emptied.

The trap holding area was about 3 m. wide, 3 m. long, and 2.4 m. deep. It was equipped with a metal brail that was divided into four sections by wooden separators (fig. 11) to facilitate the removal of captured fish. The brail was lifted by a wire rope attached to an electric winch.

EVALUATION FACILITIES

Facilities for evaluating the fish-guiding efficiency of the electrical system were about 150 m.

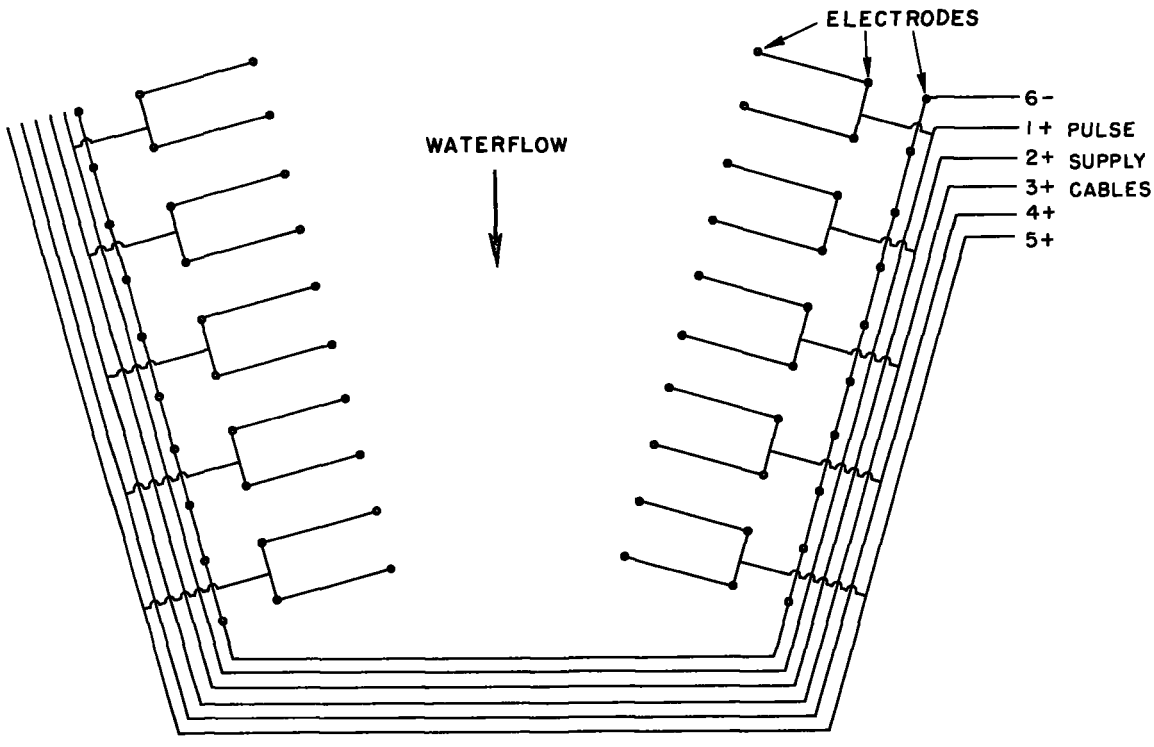

FIGURE 7.—Wiring pattern of electrode array.

downstream from the electrode array trap. All fish escaping past the electrode array were stopped by revolving drum screens (fig. 12), which diverted them to an underground bypass leading to an inclined-screen trap. Four wooden troughs adjacent to the inclined-screen trap held the captured fish while they were being counted and identified. These troughs were 20.3 cm. deep, 22.9 cm. wide, and 167.6 cm. long (fig. 13). Each was divided into three sections by removable screen partitions and fitted with an overflow standpipe at one end. A constant flow was fed to the troughs from a headbox upstream from the inclined-screen trap. The troughs were placed so the end with the standpipe was above an open flume which carried water from the inclined-screen trap to the Yakima River.

EXPERIMENTAL DESIGN

The variables tested were three water velocities (0.2, 0.5, and 0.8 m.p.s.), four test periods (variations among the test periods were due to uncontrollable environmental changes such as temperature, turbidity, and water resistivity), and three species of fish—chinook salmon, *Oncorhynchus tshawytscha;* coho salmon, *O. kisutch;* and rainbow-steelhead trout, *Salmo gairdneri.*[2] Table 2 shows the sequence of tests. The effect of each water velocity on the fish-guiding efficiency of the electrode array was tested once during each period. The experiment ran 50 days (April 21 to June 9, 1962); testing was continuous except for a 1-day interruption due to power failure during an electrical storm.

The effect of each of the three water velocities on the fish-guiding efficiency of the electrical system was determined by comparing the number of individuals of each of the three species of fish captured in the electrode array trap during a specific test period with the total number of the same species taken by the array trap plus the inclined-screen trap during that period.

Water conditions in the experimental canal were checked periodically. Velocity was measured every 2 hours with a Gurley current meter (No. 622–E)[3] at the downstream end near the middle of the

[2] The term rainbow-steelhead trout, as used in this paper, includes both seaward migrants and residual members of the species.

[3] Trade names referred to in this paper do not imply endorsement of commercial products by the Bureau of Commercial Fisheries.

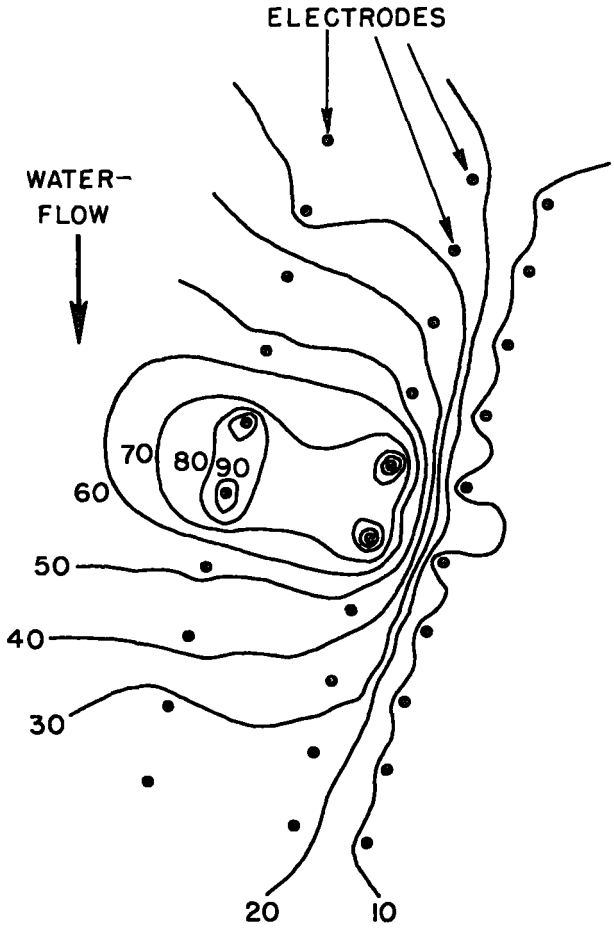

FIGURE 8.—Electrical field created by one pulse at one specific location on the left side of the electrode array. (Lines connect points of equal potential; numbers show percentage of the applied voltage.)

canal. Water temperature was taken three times daily (6:00 a.m., 2:00 p.m., and 10:00 p.m.) with a standard mercury thermometer. The average water temperature was 14.4° C. (range 11.1 to 20.0° C.). Turbidity and resistivity were also measured three times daily. Turbidity averaged 15.6 parts per million silica dioxide (range 10.0 to 26.0 p.p.m.), and the average water resistivity was 5,535 ohm cm. (range 4,290 to 7,400 ohm cm.).

To minimize the escape of fish from the array trap, the catch was removed every 2 hours (e.g., 2:00 p.m., 4:00 p.m.). Fish could not escape from the inclined-screen trap; therefore, it was checked less frequently—at 4-hour intervals (e.g., 4:00 p.m., 8:00 p.m.). This schedule was followed throughout the experiment, even during periods of

TABLE 2.—*Sequence in which different water velocities were tested during four test periods*

Test periods	Dates (1962)	Water velocities		
		M.p.s.	*M.p.s.*	*M.p.s.*
I	April 21–May 3	0.5	0.8	0.2
II	May 3–May 16	.2	.5	.8
III	May 16–May 28	.8	.2	.5
IV	May 28–June 9	.5	.8	.2

maintenance and stoplog manipulation, to ensure that fish were not delayed in their downstream migration. Fish captured in the array trap were transported in an aerated tank to the holding troughs adjacent to the inclined-screen trap where they were counted and identified. Movable partitions within the troughs made it possible to count and identify the fish without handling. The fish were released, after the data from each group had been recorded, by removing standpipes from the troughs and allowing the water and fish to drain into the bypass flume. From the flume, the fish could re-enter the Yakima River. Fish captured in the inclined-screen trap were also identified, counted, and released into the Yakima River.

EXPERIMENTAL PROCEDURE

Before beginning each test, we obtained the desired water velocity by manipulating the concrete stoplogs in the velocity control structure at the entrance to the water-bypass channel and the plywood panels in the velocity control structure in the main canal. This operation required about 8 hours.

Each control test (power off) was started at 4:00 p.m. The array trap and the inclined-screen trap were cleared of fish before the start of the test and then emptied at regular intervals for the duration. The control test lasted 40 hours (until 8:00 a.m. on the second day after the experiment started). The 8 hours following the control test (8:00 a.m. to 4:00 p.m.) were used primarily for maintenance and cleanup. At 4:00 p.m., when the maintenance period ended, the electrode array was energized according to preset electrical conditions. These conditions were monitored during the entire power-on test by means of a calibrated oscilloscope. The power-on test lasted 40 hours (until 8:00 a.m. on the second day after the array was energized); the sequential switching equipment was then turned off and the stoplogs and plywood

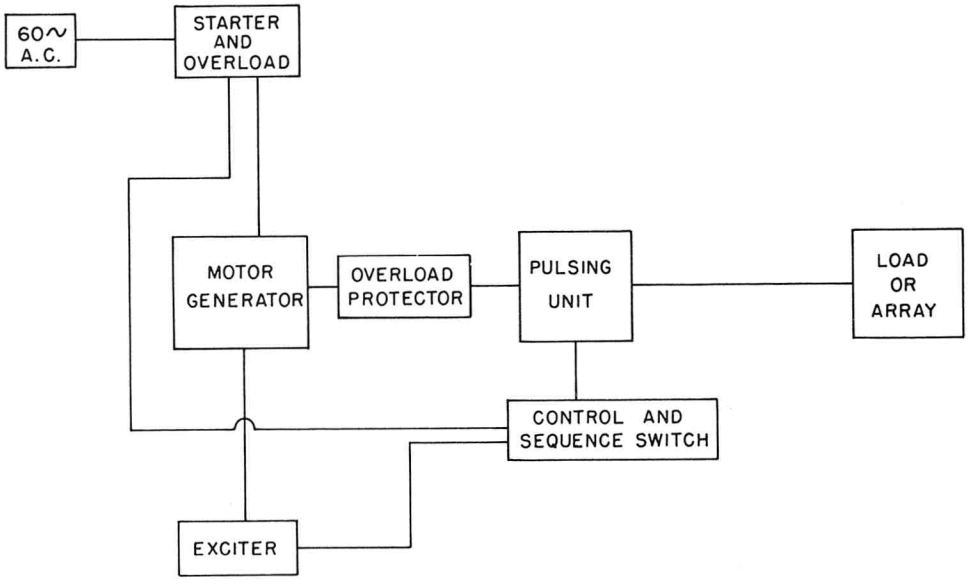

FIGURE 9.—Block diagram of sequential switching equipment used to supply d.c., square-wave pulses.

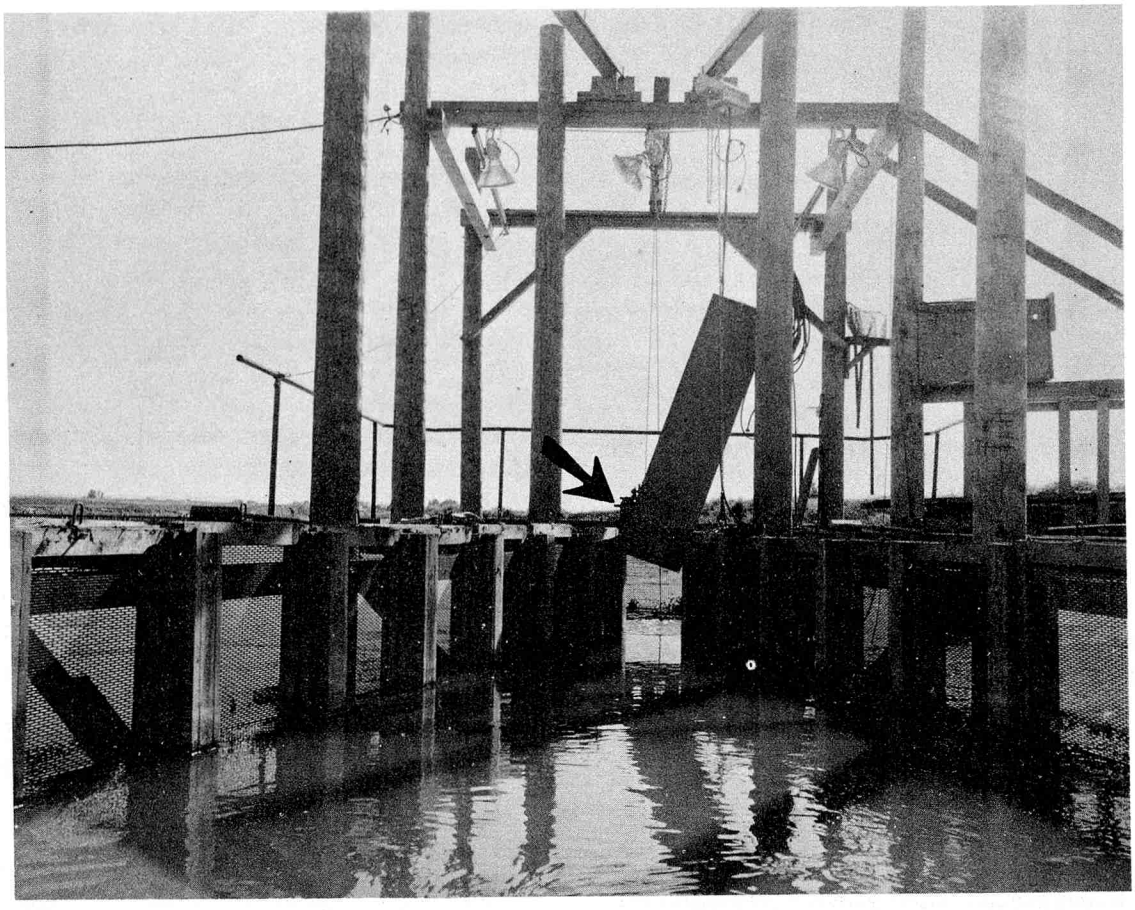

FIGURE 10.—Lead-in screens and throat (arrow) of array trap.

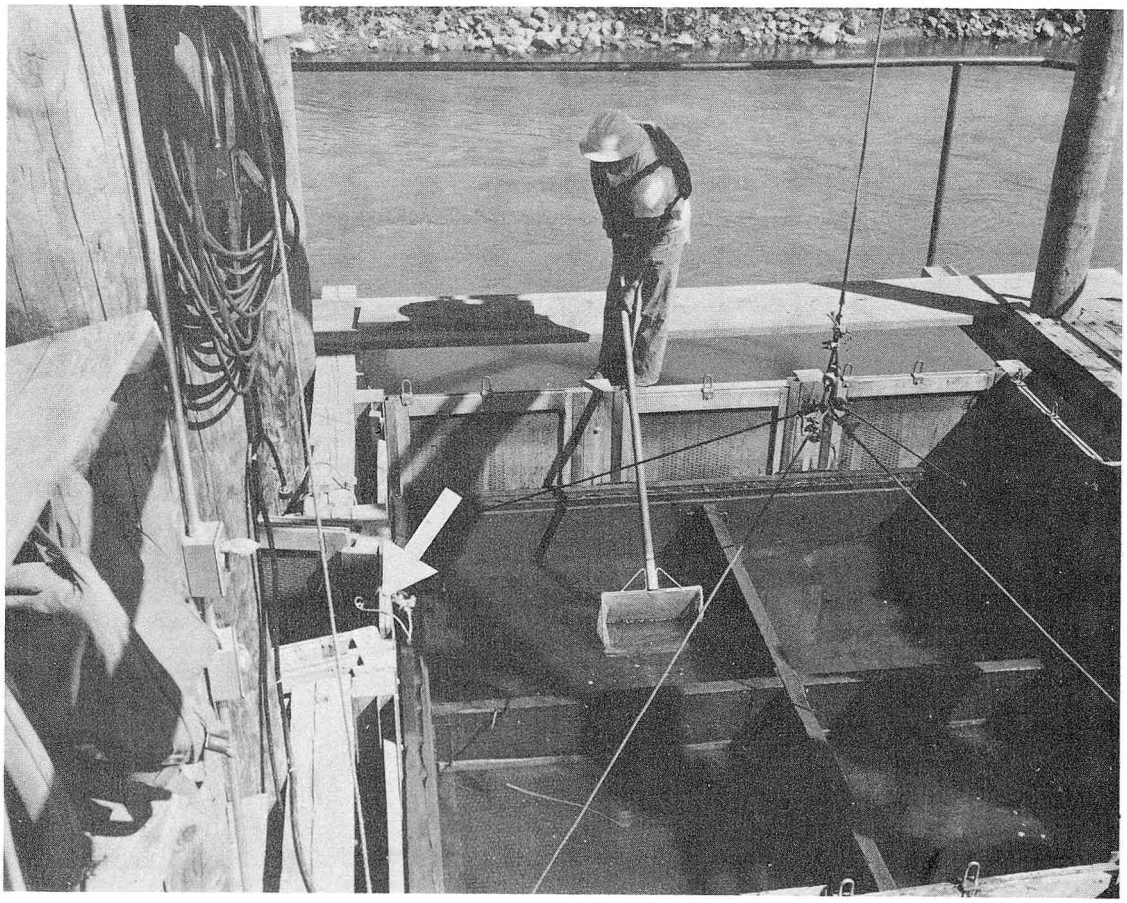

FIGURE 11.—Electrode array trap with throat closed (arrow) and sectioned brail raised.

panels manipulated to create the desired water velocity for the next test. This procedure was followed for the duration of the experiment. Each complete test took 96 hours: stoplog adjustment, 8 hours; control period, 40 hours; maintenance, 8 hours; and power-on, 40 hours.

COMPOSITION OF CATCH

Most of the test fish were wild, downstream migrants of the Yakima River system. One-hundred twenty-nine thousand juvenile salmon and trout were captured. About 50 percent were chinook salmon, 32 percent coho salmon, and 18 percent rainbow-steelhead trout. The chinook salmon belonged to age-groups 0 and I and had average fork lengths of 89 and 133 mm., respectively. The coho salmon were age-group I fish and averaged 131 mm. The rainbow-steelhead trout were age-group I and older and had a mean length of 198 mm.

EFFECT OF TEST VARIABLES ON EFFICIENCY OF FISH-GUIDING AND COLLECTING

Preliminary analysis indicated that the electrode array and array trap collected a relatively high percentage of fish, even during the power-off (control) conditions. To distinguish between the fish-collecting efficiency of the total guiding system (electrode array and array trap) with the power on and the actual fish-guiding efficiency of the electrode array and electrical field alone, the experimental results are presented in three sections: (1) electrode array energized plus array trap—percentage of fish collected by the electrode array and array trap with the electrode array energized, (2) electrode array nonenergized plus array trap—percentage of fish collected by the electrode array and array trap under control conditions, and (3) electrode array energized without

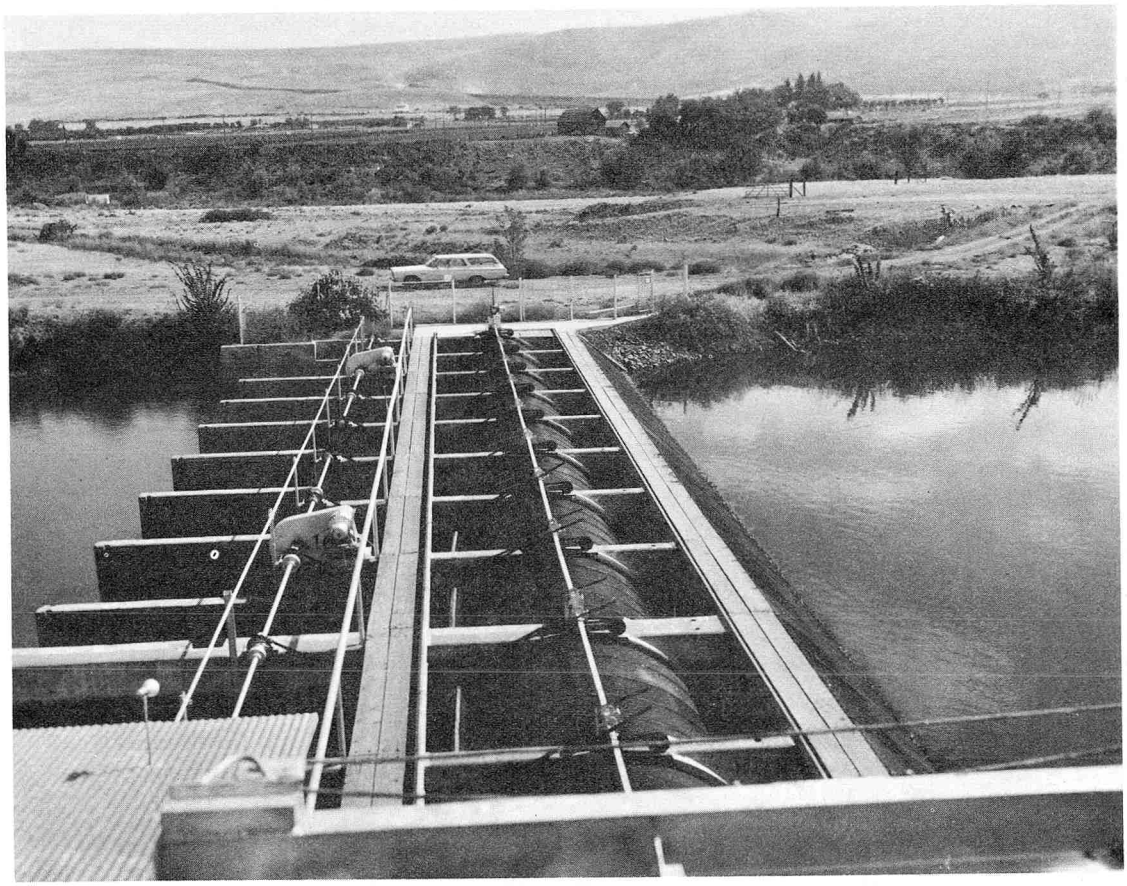

FIGURE 12.—Revolving drum screens used to divert fish that escaped past the electrode array to an inclined-screen trap.

array trap—percentage of fish actually guided by the electrode array and the electrical field created by the electrode array. Details of the methods used to compute these fish-guiding and collecting efficiencies are discussed below.

ELECTRODE ARRAY ENERGIZED PLUS ARRAY TRAP

Table 3 shows the fish-collecting efficiency of the electrode array and array trap with the power on for each test velocity and test period, by fish species. These efficiencies (in percentages) were computed by dividing the total number of each species of fish captured in the electrode array trap during a specific power-on period by the sum of this number plus the number of fish of the same species captured in the inclined-screen evaluation trap during the same power-on period, and multiplying the quotient by 100.

The mean fish-collecting efficiency for the electrode array and array trap with the power on was highest at a water velocity of 0.2 m.p.s.; intermediate at 0.8 m.p.s.; and lowest at 0.5 m.p.s. (fig.

TABLE 3.—*Fish-collecting efficiency (in percent) of the electrode array and array trap, with the electrode array energized, for each water velocity, test period, and fish species*

Velocity	Test period	Species		
		Chinook salmon	Coho salmon	Rainbow-steelhead trout
M.p.s.		*Percent*	*Percent*	*Percent*
0.2	1	88.2	82.0	71.3
	2	81.2	82.8	74.3
	3	78.2	86.0	75.9
	4	93.9	82.0	64.1
	Average	85.4	83.2	71.4
.5	1	77.1	77.9	43.3
	2	79.7	82.3	64.2
	3	72.6	60.5	59.8
	4	39.9	24.6	28.9
	Average	67.3	61.3	49.0
.8	1	88.2	76.2	74.9
	2	87.5	75.5	70.2
	3	86.4	76.1	72.2
	4	57.3	59.4	49.5
	Average	79.8	71.8	66.7

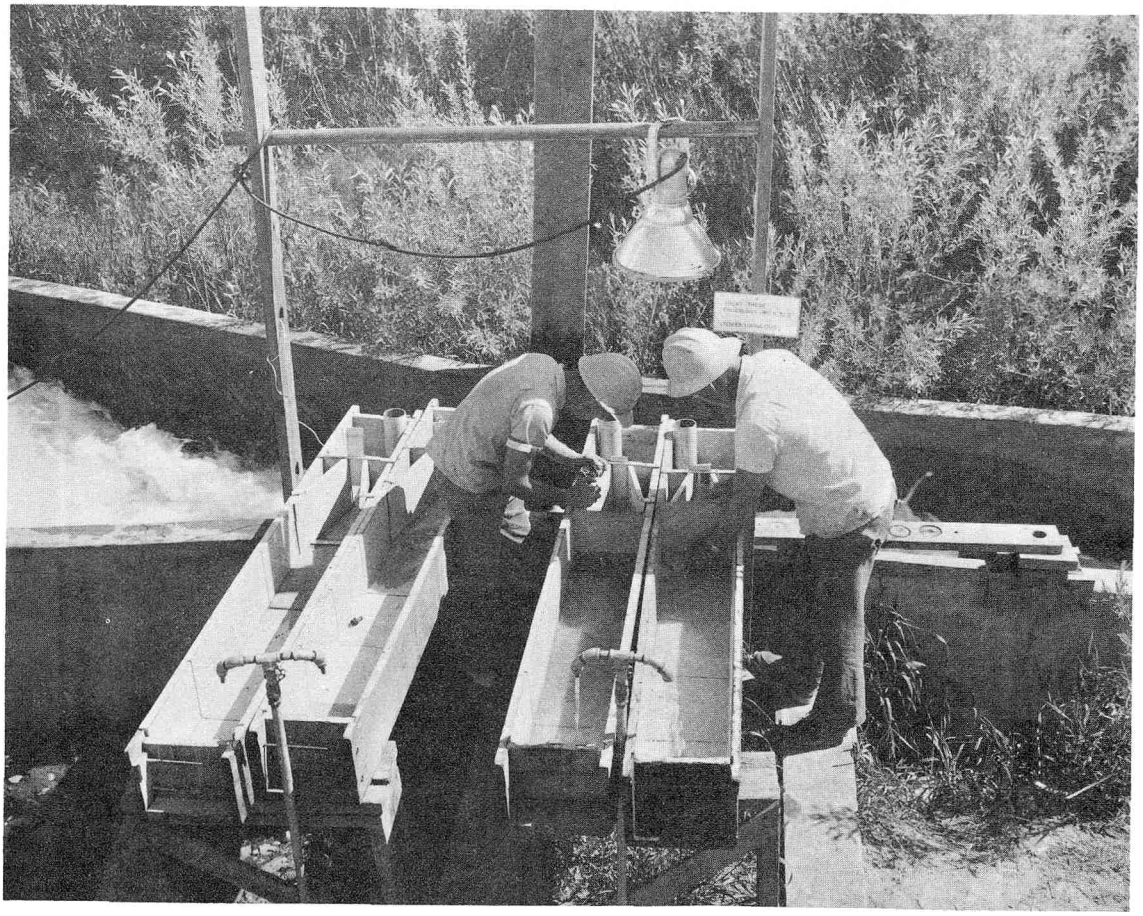

FIGURE 13.—Troughs for counting and identifying salmon and trout.

14). The decrease in fish-collecting efficiency between 0.2 and 0.5 m.p.s. and the increase at 0.8 m.p.s. suggests that fish-guiding efficiency decreased as the water velocity increased, but that perhaps: (1) the electrodes created hydraulic conditions that diverted more fish into the array trap at a water velocity of 0.8 m.p.s. than at 0.5 m.p.s. or (2) that the fish-holding efficiency of the array trap was higher at 0.8 m.p.s. than at 0.5 m.p.s. It was not possible within the scope of this research to determine the effect of the hydraulic conditions created by the electrodes on the fish-guiding efficiency of the electrical system, nor was it possible to determine conclusively the holding efficiency of the array trap at each of the three test velocities. Because salmon and trout populations of the Yakima River at the time of this experiment were so critically low, we deemed it inadvisable to handle, mark, and delay the number of migrating salmon and trout required to determine accurately the efficiency of the array trap in retaining fish.

General observations, however, indicated that fish could escape from the array trap at all test velocities but that fish-holding efficiency was higher at 0.5 m.p.s. and at 0.8 m.p.s. than at 0.2 m.p.s. Therefore, during the power-on tests, some fish were probably guided into the array trap by the electrical system but, because they were not removed immediately, they were able to escape by swimming back upstream into the canal. Consequently, all of the fish-guiding and collecting efficiencies reported here for the low and middle water velocities are probably lower than the actual efficiencies achieved. Those reported for the highest water velocity, 0.8 m.p.s., are probably more accurate than those for the lower velocities, but even these values are doubtless below the actual values achieved.

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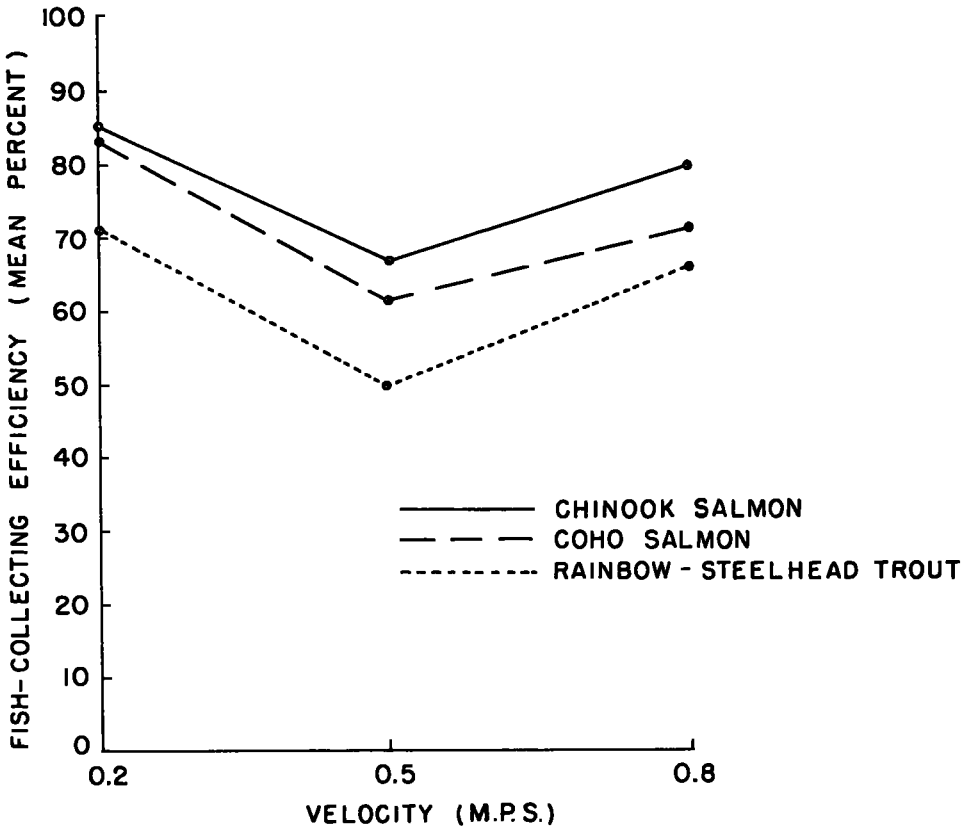

FIGURE 14.—Fish-collecting efficiency (mean percent) of the electrode array and array trap, with the electrode array energized, for each water velocity and fish species.

Figure 14 shows that the mean fish-collecting efficiency was highest for chinook salmon, intermediate for coho salmon, and lowest for rainbow-steelhead trout.

Examination of table 3 shows that at the 0.2 m.p.s. velocity, the results were about the same in the fourth test period as in the first three. At the middle and high water velocities, however, the fish-guiding and collecting efficiencies were substantially lower during the fourth test period than during the first three. To determine the reason for this decrease, we considered such factors as the size of fish, timing in the migration period, environmental fluctuations, possible malfunctions of the electronic equipment, and underwater damage to the electrode array trap. None of these factors, however, were sufficiently different from previous conditions to provide an explanation for the lower fish-guiding efficiencies. (It should be noted that the sudden unexplained failures in fish guidance at the middle and high water velocities did not occur at 0.2 m.p.s., which was the last velocity tested during the fourth test period—see table 2.)

ELECTRODE ARRAY NONENERGIZED PLUS ARRAY TRAP

We calculated the fish-collecting efficiency of the electrode array and array trap with the power off (table 4) for each test velocity and test period, by fish species, by the same method used to determine the fish-collecting efficiency of the electrode array and array trap with the power on. The catches compared were those made under control conditions. Figure 15 shows that the fish-collecting efficiency (mean percent) of the electrode array and array trap with the power off increased for all three species as the velocity increased. This increase in fish-collecting efficiency with increasing velocity during tests with the power off substantiates one or both of our previous hypotheses that: (1) the electrodes created hydraulic conditions at the higher water velocities that diverted fish into

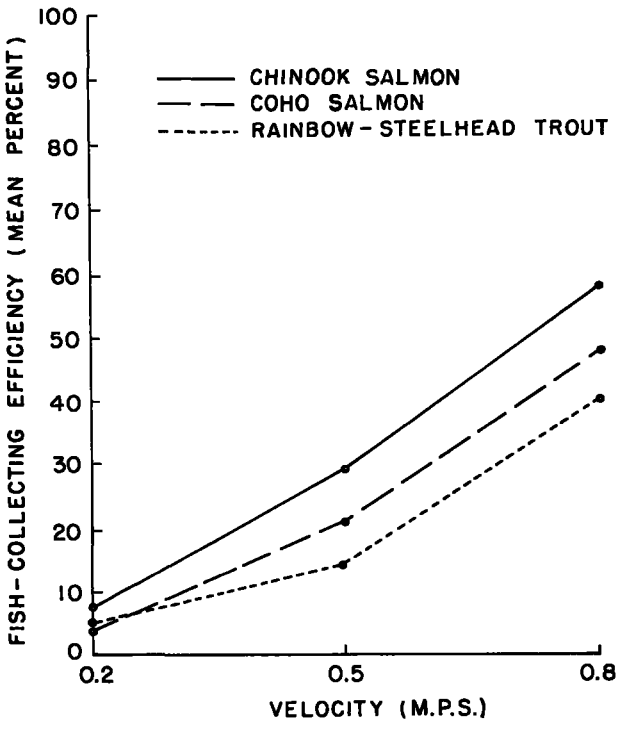

FIGURE 15.—Fish-collecting efficiency (mean percent) of the electrode array and array trap during the control conditions (power off) for each water velocity and fish species.

the array trap or (2) the fish-holding efficiency of the array trap increased with increased water velocity. In general, the rank of the species in relation to fish-collecting efficiency of the electrode array and array trap was the same as during the power-on test; chinook salmon ranked first, coho salmon second, and rainbow-steelhead trout third.

TABLE 4.—*Fish-collecting efficiency (in percent) of the electrode array and array trap during the control conditions (power off) for each water velocity, test period, and fish species*

Velocity	Time period	Species		
		Chinook salmon	Coho salmon	Rainbow-steelhead trout
M.p.s.		*Percent*	*Percent*	*Percent*
0.2	1	6.6	2.4	4.4
	2	10.5	10.2	12.3
	3	5.0	3.7	2.1
	4	5.7	2.8	1.3
	Average	7.0	4.8	5.0
.5	1	29.2	45.0	16.5
	2	30.2	23.6	14.1
	3	23.8	19.1	6.2
	4	30.0	22.0	18.0
	Average	28.3	27.4	13.7
.8	1	58.5	70.5	47.3
	2	56.8	45.2	44.6
	3	64.8	44.2	39.6
	4	58.6	33.0	31.3
	Average	59.7	48.2	40.7

ELECTRODE ARRAY ENERGIZED WITHOUT ARRAY TRAP

Fish-guiding efficiency of the electrode array (power on), without the array trap, is presented in table 5 as percentage differences between the fish-guiding and collecting efficiency of the electrode array and array trap with the power on and the efficiency with the power off. Table 5, however, is only an indication of the actual fish-guiding efficiency of the electrical guiding system. As previously mentioned, fish swimming more than 0.9 to 1.2 m. from the electrodes were not visibly affected by the electrical field created by the electrode array. As the entrance to the array trap was 6.4 m. wide, it was possible for fish migrating near the middle of the experimental canal (i.e., near the middle of the trap entrance) to enter the array trap without having been diverted by the electrical energy. These fish, therefore, were not actually available to be guided by the electrical system. Assuming that the same percentage of fish entered the array trap naturally (i.e., without being guided) during the power-on conditions as during the control periods, we established the following relations to determine the actual fish-guiding efficiency of the electrical system alone:

Let AT_p = Total number of fish captured in the array trap on any given power-on day.

IST_p = Total number of fish captured in the inclined-screen trap on the same power-on day.

AT_o = Total number of fish captured in the array trap on the preceding power-off day.

IST_o = Total number of fish captured in the inclined-screen trap on the same power-off day.

P_E = Percentage of fish guided by the electrical system that were actually available to be guided; i.e., fish that would not have entered the array trap naturally.

$$\text{Then } P_E = \frac{AT_p}{AT_p+IST_p} - \frac{\left[\frac{(AT_o)}{(AT_o+IST_o)}(AT_p+IST_p)\right]}{\left[\frac{(AT_o)}{(AT_o+IST_o)}(AT_p+IST_p)\right]} \times 100$$

TABLE 5.—*Fish-guiding efficiency (in percent) of the electrode array (power on), without the array trap, for each water velocity, test period, and fish species; values were determined by subtracting percentage of fish collected with the power off from percentage guided with the power on*

Velocity	Time period	Species		
		Chinook salmon	Coho salmon	Rainbow-steelhead trout
M.p.s.		*Percent*	*Percent*	*Percent*
0.2	1	81.6	79.6	67.0
	2	70.7	72.7	62.0
	3	73.1	82.3	74.0
	4	88.3	79.2	63.0
	Average	78.4	78.5	66.5
.5	1	47.9	32.9	27.0
	2	49.5	58.7	50.2
	3	48.7	41.4	54.0
	4	10.0	2.6	11.0
	Average	39.0	33.9	35.6
.8	1	29.6	5.7	27.6
	2	30.7	30.3	25.6
	3	21.6	31.9	32.6
	4	−1.3	26.4	18.2
	Average	20.2	23.6	26.0

Table 6 was prepared from the above formula and shows, by fish species, the adjusted fish-guiding efficiency of the electrical system for each experimental condition. Figure 16 shows the mean percentage fish-guiding efficiency of the electrode array (power on), without the array trap, for each test velocity and species. In general, efficiency was inversely related to velocity—it was highest at 0.2 m.p.s., second highest at 0.5 m.p.s., and lowest at 0.8 m.p.s. Mean guiding efficiency by species was highest for chinook salmon, intermediate for coho salmon, and usually lowest for rainbow-steelhead trout.

QUALIFICATIONS OF COMPUTATION METHODS

Because the inclined-screen trap was several hundred meters downstream from the array trap, a slight delay existed between the time that fish of a particular school or group entered the array trap and the remainder of that school or group entered

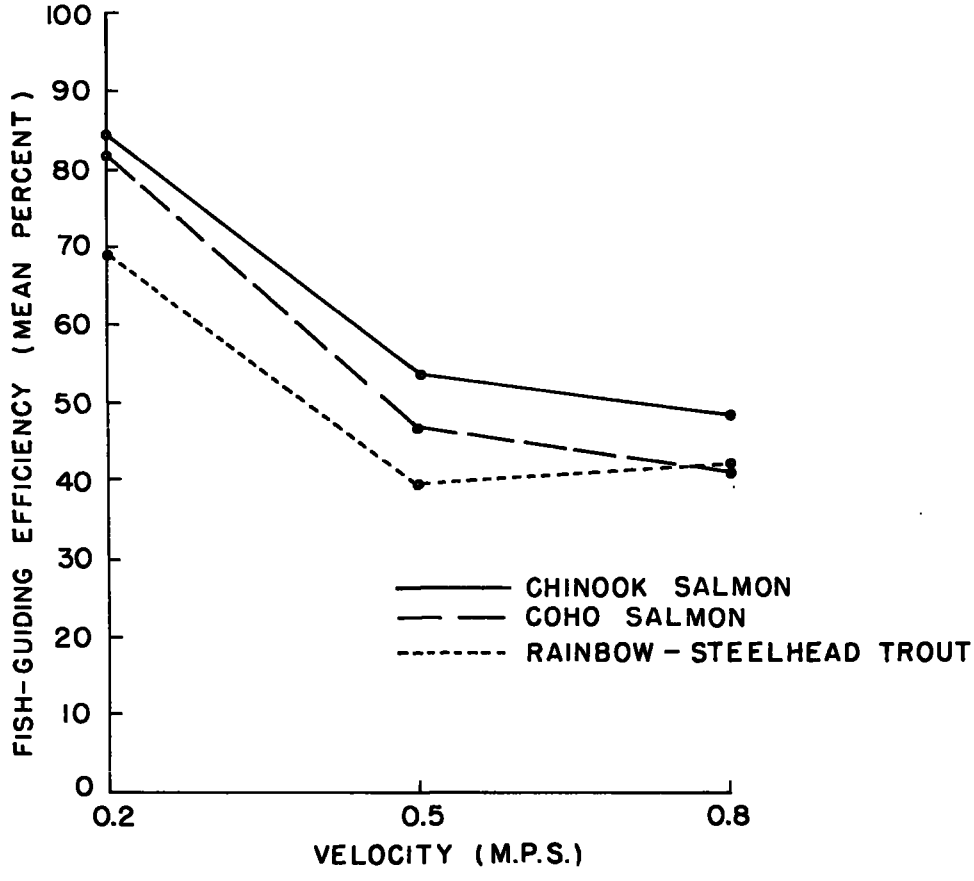

FIGURE 16.—Fish-guiding efficiency (mean percent) of the electrode array (power on), without the array trap, for each water velocity and fish species.

the inclined-screen trap. Tests to determine the exact time involved in this delay were not conclusive but indicated that the delay was usually less than 4 hours and often even less than 1. Although the array trap was checked every 2 hours and the inclined-screen trap every 4, we computed the fish-guiding and collecting efficiencies by grouping the fish captured in each trap during a 24-hour period and then comparing these totals.

TABLE 6.—*Adjusted fish-guiding efficiency (in percent) of the electrode array (power on), without the array trap, for each water velocity, test period, and fish species*

Velocity	Time period	Species		
		Chinook salmon	Coho salmon	Rainbow-steelhead trout
M.p.s.		*Percent*	*Percent*	*Percent*
0.2	1	87.4	81.5	70.0
	2	79.0	80.9	70.7
	3	77.0	85.4	75.4
	4	93.6	81.5	63.6
	Average	84.2	82.4	69.9
.5	1	67.7	59.8	32.0
	2	70.9	76.8	58.4
	3	64.0	51.2	57.1
	4	14.3	3.4	13.3
	Average	54.2	47.8	40.2
.8	1	71.5	19.2	52.4
	2	71.1	55.3	46.2
	3	61.3	57.1	54.0
	4	−3.1	39.4	26.5
	Average	50.2	42.8	44.8

Consequently, the delay time due to the distance between the two traps affected only the data for the last inclined-screen trap catch in each 24-hour period. Therefore, no lag time was allowed in computing any of the fish-collecting efficiencies. The total number of fish captured in the array trap from 12:00 midnight to the following 12:00 midnight was compared with the total number of fish captured in the inclined-screen trap during the same period. When we analyzed the data to allow for a 4-hour delay (comparing catches in the array trap between 12:00 midnight and the following 12:00 midnight with catches in the inclined-screen trap between 4:00 a.m. and the following 4:00 a.m.) and an 8-hour delay (comparing catches in the array trap between 12:00 midnight and the following 12:00 midnight with catches in the inclined-screen trap between 8:00 a.m. and the following 8:00 a.m.), the results did not modify our major conclusions.

CONCLUSIONS

We have two major conclusions:

1. The fish-guiding efficiency of the electrical system generally decreased as water velocity increased, probably because juvenile salmon and trout may be progressively less able to control their movements as velocity increases.

2. The use of electricity to guide juvenile salmon and trout migrating downstream may be feasible in certain environments where the water velocity does not exceed 0.3 m.p.s., but does not appear practical for use in most rivers and streams.

ACKNOWLEDGMENTS

The Bureau of Reclamation allowed us to use the Chandler Canal near Prosser, Wash., as our experimental site. The Washington State Departments of Fisheries and Game cooperated by permitting us to experiment on natural, downstream migrating fish of the Yakima River system. Winston Farr designed the velocity control and fish-capturing facilities, and Holbrook L. Garrett designed and supervised the construction of the electrode array. William S. Davis, Jr., planned the experimental design, and Charles C. Gillaspie constructed the electrical equipment and was responsible for its operation and maintenance.

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REVISION OF THE GENUS *SYMPHYSANODON* (PISCES: LUTJANIDAE) WITH DESCRIPTIONS OF FOUR NEW SPECIES[1]

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ABSTRACT

The genus is redescribed; four new species — two from the western Atlantic and two from the Pacific — are described; *S. typus*, from the Pacific and until recently the only known species of the genus, is redescribed; and a key to the species is provided. Discussions are presented on the systematic position of the genus, the synonymies of species, and the zoogeography and phylogeny of the genus; species are compared; and brief comments are made on distributions.

Two new species of *Symphysanodon* (Pisces: Lutjanidæ) have been collected in the West Indies and Caribbean Sea during cruises of the research vessels *Combat*, *Oregon*, *Silver Bay*, and *Undaunted* of the FWS (U.S. Fish and Wildlife Service) and the *Gerda* and *John Elliott Pillsbury* of the Institute of Marine Sciences, University of Miami. A third new species has been collected off Hawaii—off a lava flow by William A. Gosline and coworkers and during cruises of the FWS research vessel *Townsend Cromwell* by Paul J. Struhsaker. A fourth new species has been obtained off Japan by students of Kochi University. Until the discovery of the Atlantic species, this genus was known only from the Kai Islands, New Guinea, the Philippines, Japan, and Hawaii. Three scientific names have been proposed for Pacific *Symphysanodon;* this study shows that all three apply to the same species (*S. typus*). Anderson (1967) mentioned two undescribed species of *Symphysanodon* from the western Atlantic and presented a key for their separation; they are described herein.

The following abbreviations are used: AM, The Australian Museum (Sydney); AMNH, The American Museum of Natural History; ANSP, The Academy of Natural Sciences of Philadelphia; BLBG, BCF (Bureau of Commercial Fisheries) Biological Laboratory (Brunswick, Ga.); BPBM, Bernice P. Bishop Museum (Honolulu, Hawaii); BMNH, British Museum (Natural History); BOC, Bingham Oceanographic Collections, Yale University; CU, Cornell University; FMNH, Field Museum of Natural History (Chicago, Ill.); HBL, BCF Biological Laboratory (Honolulu, Hawaii); IRSNB, Institut Royal des Sciences Naturelles de Belgique (Brussels); LACM, Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Museum National d'Histoire Naturelle (Paris, France); RMNH, Rijksmuseum van Natuurlijke Historie (Leiden, Netherlands); SU, Stanford University; TABL, BCF Tropical Atlantic Biological Laboratory (Miami, Fla.); TU, Tulane University; UF, Florida State Museum, University of Florida; UH, University of Hawaii; UMML, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami; UMMZ, Museum of Zoology, The University of Michigan; USNM, U.S. National Museum; UW, College of Fisheries, University of Washington; YU, Yamaguchi University (Yamaguchi City, Japan); ZIKU, Zoological Institute, Kochi University (Kochi, Japan); and ZSZM, Zoologisches Staatsinstitut und Zoologisches Museum (Hamburg, West German Federal Republic). SL designates standard length.

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Published October 1970.

METHODS

Measurements and counts were made according to the methods of Hubbs and Lagler (1958), except for the following: depth of head was measured just posterior to orbit; length of orbit, as longest horizontal distance between fleshy margins of orbit; width of bony interorbital, above vertical midline of eye; depth of body, from origin of first dorsal spine vertically to ventral surface of body; and lengths of caudal fin lobes, from middle of origin of caudal fin to distal ends of longest rays. The last ray of dorsal and anal fins was counted as one when branched to the base.

Pelvic fins and caudal-fin lobes with long filaments were difficult to measure. Some of the filamentous fins were measured by stretching them out along a meter stick. Other measurements were made with needlepoint-micrometer-dial calipers. When the two pectoral and two pelvic fins were of unequal length, the longer fin was measured.

Where possible, gill rakers (including rudiments, when present) on the anterior gill arch and pectoral-fin rays were counted on the right side, pored lateral-line scales on the left side.

Most specimens had lost many scales and consequently accurate counts of pored lateral-line scales were made on fewer than a third of those examined. Approximate counts of lateral-line scales were recorded for a number of specimens. Accurate and approximate counts of scales are combined in table 1 and distinguished in table 2.

GENUS *SYMPHYSANODON* BLEEKER

Symphysanodon Bleeker, 1878: 60—also p. 26 in author's undated reprint—(type species *Symphysanodon typus* Bleeker, 1878, by original designation—by virtue of the name *typus*).

Propoma Günther, 1880: 39 (type species *Propoma roseum* Günther, 1880 [= *Symphysanodon typus* Bleeker, 1878], by monotypy).

Rhyacanthias Jordan, 1921: 646 (type species *Rhyacanthias carlsmithi* Jordan, 1921 [= *Symphysanodon typus* Bleeker, 1878], by original designation).

Snout relatively blunt. Anterior ends of premaxillaries incised, forming a conspicuous notch —the notch receiving the anterior ends of the dentaries. Extreme dorsalmost margin of maxillary covered by very narrow suborbital with mouth closed. Mouth terminal; mandible inclined dorsally when mouth closed; jaws about equal. A bony elevation (which may be pronounced) on posterodorsal surface of dentary. Two narial openings on each side. Pseudobranchiæ present. Gill arches four, a slit behind the fourth. Premaxillary with small teeth—usually larger anteriorly; premaxillary notch toothless. Dentary with small teeth usually extending from bony elevation almost to the symphysis; teeth on and near bony elevation usually larger; usually a number of relatively large, exserted teeth at anterior end of dentary—these teeth fitting into notch in upper jaw when mouth closed; symphysis toothless. Teeth, when present, on vomer, palatines, and pterygoids small; no teeth on tongue. Dorsal fin continuous and not incised at junction of spines and soft rays. Opercle with two flattened spines, the ventral one longer and more prominent. Scales ctenoid; posterior part of snout, interorbital, preorbital, suborbital, maxillary, ventral surface of mandible, preopercle, interopercle, opercle, and subopercle with scales; dorsal and anal fins without scales, but with scaly sheaths at their bases; large modified scales associated with pelvic fins, just dorsal to each pelvic spine (axillary scales) and in the ventral midline between the pelvic fins somewhat overlapping their anteromedial borders. Lateral line gently curved beneath the dorsal fin; cephalic lateral-line system well developed. Pronounced sexual dimorphism in at least one species (and probably in two).

Dorsal-fin rays usually IX, 10. Anal-fin rays III, 7 or 8. Pectoral-fin rays 15 to 18. Pelvic-fin rays I, 5. Principal caudal-fin rays 17 (9 + 8). Vertebrae 25 (10 precaudal + 15 caudal). Branchiostegal rays 7. Gill rakers well developed, rather long and slender, 9 to 14 + 22 to 29—total on anterior gill arch 31 to 42. Pored lateral-line scales 43 to 54.

SYSTEMATIC POSITION OF THE GENUS *SYMPHYSANODON*

Symphysanodon, which has been variously considered as a serranid or as a lutjanid, superficially resembles the members of the serranid subfamily Anthiinæ and is unlike (in at least its superficial appearance) the more generalized lutjanids, such as *Lutjanus* and its allies. Kamohara and Katayama (1959) placed *Symphysanodon* in the subfamily Anthiinæ of the Serranidæ; Katayama (1960) placed it in the Serranidæ, but did not refer it to a subfamily. Gosline and Brock (1960) and Munro (1967) included this genus with the Lutjanidæ.

Gosline (1966) provisionally combined a number of serranid subfamilies (sensu Katayama, 1960) along with certain genera (such as *Roccus* and *Percichthys*) into the family Percichthyidæ, but retained the subfamily Anthiinæ (sensu Katayama, 1960) in the Serranidæ. He excluded *Symphysanodon* from the Serranidæ, but did not allocate it to a family. Gosline did note, however, that *Symphysanodon* shows a closer resemblance to lutjanids than to serranids in fin-ray counts and in the possession of parietal crests and well-developed axillary scales associated with the pelvic fins.

On the basis of a number of osteological characters Katayama (1968) stated that *Symphysanodon* resembles the Percichthyidæ (of Gosline, 1966) more than the Serranidæ (as restricted by Gosline, 1966). Katayama (1968) mentioned that *Symphysanodon* differs from the Lutjanidæ in the myodome not opening to the exterior through a foramen, in the sensory canal of the frontal bone lacking an inner branch connecting with the corresponding one of the opposite side, in having an oblong foramen near the upper margin of the ceratohyal, and in having 25 vertebrae. (Most Lutjanidæ have 24 vertebrae. According to Gosline (1966), the Percichthyidæ have 25 vertebrae—frequently more, members of the Anthiinæ tend to have 26, and the other subfamilies of the Serranidæ— the Epinephelinæ and the Serraninæ—have 24.) Katayama (1968) also listed a number of osteological structures of *Symphysanodon* which are more similar morphologically to the corresponding structures of the Lutjanidæ than to those of the Percichthyidæ. These structures are: jaw bones, suspensorium and opercular apparatus, pectoral girdle, and pelvic girdle. In addition, he noted that *Symphysanodon* is closer to the Lutjanidæ (than to the Percichthyidæ) in possessing fronto-parietal crests and axillary scales associated with the pelvic fins. In concluding his paper on *Symphysanodon*, Katayama (1968) remarked that he ". . . would like to place *Symphysanodon typus* Bleeker under Lutjanidæ . . ." and that this genus seems to be closely related to the members of the subfamily Etelinæ.

On the basis of the studies by Gosline (1966) and Katayama (1968) and my own investigations, I assign *Symphysanodon* to the Lutjanidæ (in which its greatest affinities are with the Etelinæ).

KEY TO THE SPECIES OF *SYMPHYSANODON*

Gill-raker counts are of the total number on the anterior gill arch (including rudiments, when present); scale counts are of the number of pored lateral-line scales on the body (excluding those posterior to the caudal base); gill-raker and scale counts of individual specimens appear to be correlated (see table 1).

A. Depth of body 2.8 to 3.0 times in SL (33.4–36.0 percent SL). Anal soft rays usually 8 (7 in about 10 percent of specimens examined). Gill rakers 39 to 42. Scales 45 or 46 ..... *octoactinus*, western Atlantic.

TABLE 1.—*Relation of total number of gill rakers on anterior gill arch to number of pored lateral-line scales in* Symphysanodon

[t = *S. typus*; k = *S. katayamai*; m = *S. maunaloae*; b = *S. berryi*; o = *S. octoactinus*; numbers within the body of the table represent the individuals with each gill raker-scale combination]

Total gill rakers	43	44	45	46	47	48	49	50	51	52	53	54
42				o1								
41			o3									
40				o1								t1
39			o1				b1	b1				
38						b2	b2		b1	b1	t1	t1
37				m1		b1	b2	b3		t2	t1	
36	m1					b6	b6	b1	b1			
35						b1	b4	k1 b5	b2			
34			m1	m2	m1		b2	b1				
33	m1		m1	m2	m3							
32		m1	m1	m1	m1							
31			m1									

Lateral-line scales

AA. Depth of body 3.2 to 4.7 times in SL (21.3–ca. 31 percent SL). Anal soft rays 7. Gill rakers 31 to 40. Scales 43 to 54 ..... B

B. Anal fin long, length of depressed anal fin 2.6 times in SL (ca. 39 percent SL). Depth of body 3.2 times in SL (ca. 31 percent SL) ..... *katayamai*, Japan.

BB. Anal fin short, length of depressed anal fin 3.1 to 4.4 times in SL (22.8–32.6 percent SL). Depth of body 3.4 to 4.7 times in SL (21.3–29.0 percent SL) C

C. Scales 43 to 47. Gill rakers 31 to 37. Sum of gill rakers plus scales 76 to 81, 83 ..... *maunaloæ*, Hawaii.

CC. Scales 48 to 54. Gill rakers 34 to 40. Sum of gill rakers plus scales 83 to 92, 94 ..... D

D. Scales 48 to 51 (rarely 52). Gill rakers 34 to 39. Pectoral-fin rays 16 to 18, usually 17. Vertical limb of preopercle usually with well-developed serrae at all sizes; usually a single spine (most frequently serrate, often bifid) or spinelike process at angle of preopercle. First pelvic soft ray noticeably produced in males larger than ca. 85 mm. SL, extremely filamentous in large males. Caudal-fin lobes frequently produced into excessively long filaments in large males ..... *berryi*, western Atlantic.

DD. Scales 52 to 54. Gill rakers 36 to 38, 40. Pectoral-fin rays 15 to 17, usually 16. Vertical limb of preopercle with small serrae in small specimens (80 mm. SL or smaller), finely serrate, slightly roughened, or almost smooth in specimens larger than 100 mm. SL; usually a well-developed spine at angle of preopercle in specimens 80 mm. SL or smaller, spine or spinelike process present or absent in specimens larger than 100 mm. SL. First pelvic soft ray only slightly produced, not extending to anal fin. Caudal-fin lobes produced, but apparently never produced into excessively long filaments ..... *typus*, New Guinea, Kai Islands, Philippine Islands, and Hawaii.

KEY TO *SYMPHYSANODON BERRYI* AND *S. TYPUS*

Measurements of certain body parts can be used to distinguish specimens of *S. berryi* and *S. typus* of similar sizes. Because I had no specimens of *S. typus* between 80 and 100 mm. SL, that size range is excluded in the following key.

A. Specimens 80 mm. SL or smaller ..... B

AA. Specimens larger than 100 mm. SL C

B. Length of depressed anal fin 22.8 to 25.8 percent SL. First anal spine 3.3 to 5.2 percent SL (usually 3.9–4.9). Length of base of anal fin 12.7 to 15.3 percent SL (usually 13.0–14.9) ..... *berryi*.

BB. Length of depressed anal fin 27.7 to 30.2 percent SL. First anal spine 5.0 to 6.2 percent SL. Length of base of anal fin 14.7 to 16.4 percent SL ..... *typus*.

C. Length of third anal spine 12.5 to 15.0 percent SL (usually 12.7–14.6). Length of second anal spine 10.6 to 13.4 percent SL (usually 10.9–13.0). Length of first anal spine 3.4 to 5.6 percent SL (usually 3.9–5.1). Length of base of anal fin 13.4 to 15.8 percent SL (usually 13.6–15.3). Length of depressed anal fin 23.4 to ca. 27.6 percent SL (usually 24.0–26.2) ..... *berryi*.

CC. Length of third anal spine 10.8 to 12.0 percent SL. Length of second anal spine 10.0 to 10.5 percent SL. Length of first anal spine 5.4 to 6.1 percent SL. Length of base of anal fin 15.6 to 20.8 percent SL. Length of depressed anal fin 26.6 to 32.6 percent SL ..... *typus*.

SYMPHYSANODON TYPUS BLEEKER

Figure 1; tables 1 to 4

Symphysanodon typus Bleeker, 1878: 61, pl. 3, fig. 1—also p. 27, pl. 2, fig. 1, in author's undated reprint—(original description and illustration; holotype ZSZM H 398, 112 mm. SL; type locality New Guinea). ..... Bleeker, 1880: 28, pl. 5, fig. 2 (description apparently based on same material as that of Bleeker, 1878, and illustration; New Guinea). ..... Jordan and Seale, 1906: 268 (reference to original description). ..... Weber and de Beaufort, 1936: 309, fig. 65 (synonymy referring in part to *S. typus* and in part to *S. maunaloæ*, compiled description [probably representing *S. typus*], illustration [after Günther, 1880], and distribution referring to *S. typus* and in part to *S. maunaloæ*). ..... Tinker,

FIGURE 1.—Holotype of *Symphysanodon typus* (ZSZM H 398), 112 mm. SL.

1944: 200, fig. (illustration [drawn from Jordan and Jordan, 1922]; notes on color, size, and distribution [based on ?]). ------- Ladiges, von Wahlert, and Mohr, 1958: 163 (listing of ZSZM H 398 from New Guinea as lectotype of *S. typus*, herein considered as an attempt to designate this specimen as the lectotype of *S. typus;* indication that ZSZM H 398 may be holotype of *S. typus*). ..... Munro, 1958: 192 (reference to original description). ..... Gosline and Brock, 1960: 183–184, 327 (at least in part; partial synonymy; characters which can be used to identify *Symphysanodon;* Hawaii). ..... Anderson, 1967: 2, 11 (compiled meristic data referring in part to *S. typus*, in part to *S. maunaloæ*, and in part to *S. katayamai;* distribution referring in part to *S. typus*, in part to *S. maunaloæ*, and in part to *S. katayamai*). ..... Munro, 1967: 288 (characters which can be used to identify *Symphysanodon;* note that *S. typus* has been recorded from west New Guinea).

Propoma roseum Günther, 1880: 39, pl. 20, fig. B (original description and illustration; lectotype, herein designated, BMNH 1879.5.14.164–5, 107 mm. SL; type locality off Kai Islands). ..... Fowler, 1925: 39 (remarks concerning familial position of *Propoma roseum* Günther and similarity of *P. roseum* to *Rhyacanthias carlsmithi* Jordan).

Rhyacanthias carlsmithi Jordan, 1921: 647, fig. 3 (original description and illustration; holotype USNM 84099, ca. 148 mm. SL; type locality off a lava flow from Mauna Loa, Alika, Kau District, Hawaii). ..... Jordan and Jordan, 1922: 46, fig. 3 (reference to original description, illustration [after Jordan, 1921], and locality of collection). ..... Fowler, 1925: 39 (mention of similarity to *Propoma roseum* Günther).

Symphysodon typus, Herre, 1950: 151 (lapsus calami for *Symphysanodon;* synonymy; description of six specimens taken off the Philippines).

DIAGNOSIS

Body slender, the depth 22.1 to 29.0 percent SL. First pelvic soft ray only slightly produced, not extending to anal fin. Anal fin short, length of depressed anal fin 26.6 to 32.6 percent SL. Caudal fin deeply forked, both lobes produced, but apparently never produced into excessively long filaments. Anal soft rays 7. Gill rakers 10 to 12 + 25 to 28—total 36 to 38, 40. Pored lateral-line scales 52 to 54.

DESCRIPTION

Maxillary extending posteriorly to about middle of eye or slightly beyond. Length of upper jaw contained in length of mandible 0.95 to 1.08 times. Interorbital region flattened. Small teeth present on vomer (in a small patch), palatines (in a single band on each), and mesopterygoids (in patches) of two largest specimens (ca. 148 and 165 mm. SL)—teeth, if present, on ectopterygoids of two largest specimens confined to anterior tip of bone; teeth not apparent on vomer, palatines,

mesopterygoids, and ectopterygoids of other specimens (50–112 mm. SL). Vertical limb of preopercle with fine serrae in small specimens (80 mm. SL or smaller), finely serrate, slightly roughened, or almost smooth in specimens more than 100 mm. SL; horizontal limb of preopercle smooth or almost smooth; usually a well-developed spine at angle of preopercle in specimens 80 mm. SL or smaller, spine or spinelike process present or absent in specimens more than 100 mm. SL. Anterior part of snout and most of gular region without scales; usually one to several scales present in midline of anterior part of gular region; largest specimen examined (165 mm. SL) with a few scales on the membrane covering the fourth branchiostegal ray on each side (no other scales seen on branchiostegal membranes of this specimen), no scales apparent on branchiostegal membranes of other specimens.

Counts

Frequency distributions for the following counts are given in tables 2, 3, and 4. Dorsal-fin rays IX, 10. Anal-fin rays III, 7. Pectoral-fin rays 15 to 17. Gill rakers 10 to 12 + 25 to 28—total 36 to 38, 40. Pored lateral-line scales 52 to 54. Sum of total number of gill rakers on anterior gill arch plus number of pored lateral-line scales of individual specimens 89 to 92, 94.

(The holotype of *Rhyacanthias carlsmithi*, USNM 84099, is a dried specimen, ca. 148 mm. SL. Because the dorsal- and pectoral-fin rays and gill rakers were not counted with certainty on this specimen, data for these counts are omitted from tables 3 and 4.)

TABLE 2.—*Frequency distributions of number of pored lateral-line scales in* Symphysanodon

[The upper number in a block represents accurate counts, the lower number approximate counts]

Species	43	44	45	46	47	48	49	50	51	52	53	54	$\bar{X}$
typus	..	..	..	..	..	..	..	..	..	2	2	1	52.80
	..	..	..	..	..	..	..	..	..	1*	.	1	53.00
katayamai	..	..	..	..	..	..	..	1*	..	..	..	..	50.00
	..	..	..	..	..	..	..	..	..	..	..	..	....
maunaloae	2	..	4*	4	3	..	..	..	..	..	..	..	45.46
	..	1	..	2	2	..	..	..	..	..	..	..	46.00
berryi	..	..	..	..	..	7	10	10*	4	1	..	..	49.44
	..	..	..	..	..	3	7	6	.	.	.	..	49.19
octoactinus	..	..	3	2*	..	..	..	..	..	..	..	..	45.40
	..	..	1	..	..	..	..	..	..	..	..	..	45.00

*Includes holotype.

Measurements

Ranges of selected measurements are presented in percentage of standard length followed by the value for the holotype of *S. typus* in parentheses. For some characters variation with size is indicated. Length of head 27.7 to 33.5 (32.0)—32.2 to 33.5 in specimens 50 to 80 mm. SL, 27.7 to 32.2 in those of 105 to 165 mm. SL. Depth of head 19.1 to 24.2 (21.0)—19.1 to 21.9 in specimens 50 to 80 mm. SL, 21.0 to 24.2 in those

TABLE 3.—*Frequency distributions of numbers of fin rays in* Symphysanodon

Species	Dorsal-fin rays				Anal-fin rays		Pectoral-fin rays				
	VIII,11	IX,9	IX,10	X,10	III,7	III,8	15	16	17	18	$\bar{X}$
typus			11*	....	12*	..	1	7*	2	..	16.10
katayamai			1*	....	1*	.....		1*	.....		16.00
maunaloae		3	23*	....	26*	..	3	19*	4	..	16.04
berryi	1	1	132*	....	134*	.....		12	107*	15	17.02
octoactinus		1	17*	1	2	17*	..	18*	1	..	16.05

*Includes holotype.

TABLE 4.—*Frequency distributions of number of gill rakers in* Symphysanodon

Species	Upper limb							Lower limb									Total (= upper limb + lower limb)													
	9	10	11	12	13	14	$\bar{X}$	22	23	24	25	26	27	28	29	$\bar{X}$	31	32	33	34	35	36	37	38	39	40	41	42	$\bar{X}$
typus		2	6*	3	.....		11.09	.....		1	8*	1	1	..		26.18	.....					3	4*	3	....	1	.....		37.27
katayamai			1*	.....			11.00	.....	1*	.....						24.00	.....				1*	.....							35.00
maunaloae	4	19*	3	.....			9.96	4*	12	8	1	1	.....	.....		23.35	1	5*	11	6	1	1	1	.....					33.31
berryi	1	69	61*	3	.....		10.49	.....	9	57	50*	17	1	..		25.58	.....	9	39	39	30*	14	3	.....					36.07
octoactinus			5	12*	2		12.84	.....		1	10*	6	2			27.47	.....					6	4*	6	3				40.32

*Includes holotype.

105 to 165 mm. SL. Length of snout 6.1 to 8.2 (ca. 6.2). Horizontal diameter of fleshy orbit 8.1 to 12.0 (11.0)—ca. 11.1 to 12.0 in specimens 50 to 80 mm. SL, 8.1 to 11.0 in those 105 to 165 mm. SL. Width of suborbital 0.7 to 1.3 (ca. 1.1). Height of cheek 4.2 to 6.2 (5.4). Length of upper jaw 12.4 to 15.0 (14.2). Length of mandible 12.5 to 14.6 (14.4). Width of bony interorbital 6.6 to 8.7 (8.7). Depth of body 22.1 to 29.0 (27.0)—22.1 to 26.5 in specimens 50 to 80 mm. SL, 26.7 to 29.0 in those 105 to 165 mm. SL. Least depth of caudal peduncle 9.9 to 12.1 (10.9) —9.9 to 10.7 in specimens of 50 to 80 mm. SL, ca. 10.6 to 12.1 in those 105 to 165 mm. SL. Pectoral fin usually reaching a vertical through base of first or second dorsal soft ray; length of longer pectoral fin ca. 25.8 to ca. 29.7 (broken). Pelvic fin not extending to anal fin, first pelvic soft ray not greatly produced; length of longer pelvic fin ca. 22.3 to 25.4 (broken). Length of base of anal fin 14.7 to 20.8 (15.9)—14.7 to 16.4 in specimens 50 to 80 mm. SL, 15.6 to 20.8 in those 105 to 165 mm. SL. Length of depressed anal fin 26.6 to 32.6 (broken)—27.7 to 30.2 in specimens 50 to 80 mm. SL, 26.6 to 32.6 in those 105 to 165 mm. SL. Lengths of dorsal spines: first 4.9 to 6.3 (—),[4] second 9.3 to 10.5 (—),[4] third 10.8 to 13.6 (—),[4] fourth 11.2 to 14.6 (—),[4] longest (fifth or sixth) 11.9 to 15.7 (13.2), last 11.2 to 13.4 (—).[4] Lengths of anal spines: first 5.0 to 6.2 (6.0), second 9.5 to >10.8 (10.5), third 10.8 to 13.1 (12.0)—12.3 to 13.1 in specimens 50 to 80 mm. SL, 10.8 to 12.0 in those 105 to 165 mm. SL. Caudal fin deeply forked, both lobes produced, but apparently never produced into excessively long filaments. Length of upper lobe of caudal fin ca. 36.5 to >42 (broken). Length of lower lobe of caudal fin ca. 35.8 to >48 (broken)—based on measurements of three specimens only.

Coloration

Several color descriptions of *Symphysanodon typus* have been published. Bleeker (1878 and 1880) stated "... colore corpore pinnisque dilute roseo; iride aurantiaco-flava; caudali lobo superiore apice macula lata fusca." Günther (1880) remarked "Apparently rose coloured during life; caudal fin yellowish. Lower parts silvery." Jordan (1921) observed "Color uniform whitish when received, probably rosy silvery in life, with no markings or shades anywhere." Herre (1950) stated "Our specimens were roseate in life, turning to dull reddish brown in preservative. Thinly sprinkled over the sides are black circular dots. The fins, evidently clear red in life, are colorless to palè tan." Gosline and Brock (1960), presumably describing *S. typus*, gave the color as plain greenish.

In alcohol, specimens more than 100 mm. SL are straw colored—with some individuals showing scattered flecks of dark pigment. Specimens 80 mm. SL or smaller are darker with considerable numbers of dark pigment spots—two rows of spots on dorsal surface of caudal peduncle, sides of body with numerous spots more or less arranged in rows, many lighter punctulations scattered among the more linearly arranged larger spots (this particularly evident dorsally), head usually with relatively few spots. The caudal fin is mainly straw colored, other fins mostly pale. (Pigment spots are not easily seen without magnification.)

COMMENTS ON THE HOLOTYPE OF *SYMPHYSANODON TYPUS*

Bleeker (1878) stated that he identified 118 species of fishes during a visit to the museum at Hamburg. Three of these, including *S. typus*, were described as new. In addition, Bleeker (1878) included *S. typus* in a list of the species examined in the museum at Hamburg. He also wrote that "M. le docteur J. G. Fischer, directeur de cet établissement, a eu la complaisance de m'adresser un premier envoi, composé de collections faites à la Nouvelle-Guinée, à Singapore, au Japon, en Chine et à l'île Maurice." (There is no indication as to which species were sent to Bleeker nor whether they were sent as a loan or as a gift.)

Whitehead, Boeseman, and Wheeler (1966) stated ". . . there is no evidence that Bleeker parted with specimens from his own personal collection after his return to Holland in 1860, except in the case of the British Museum sale. Neither is there any evidence that he did so before this date." They also noted that "... types contained in material on loan from other institutions were always stated by Bleeker to have been returned."

[4] This measurement not taken on holotype.

A. C. Wheeler and M. Boeseman informed me that they could not find any specimens listed as *S. typus* in the collections of the British Museum (Natural History) (Wheeler, in litt., October 27, 1966) and Rijksmuseum van Natuurlijke Historie (Boeseman, in litt., August 7, 1967). In addition, Boeseman wrote that he did not find *S. typus* listed in Bleeker's Auction Catalogue, 1879. From the preceding it seems that if type material of *S. typus* were sent to Bleeker, it was sent on loan and later returned. All of the type material of *S. typus*, then, should be at Hamburg.

Ladiges et al. (1958) listed a specimen (at Hamburg) cataloged as ZSZM H 398 as the "lectotype (holotype?)" of *Symphysanodon typus* Bleeker, 1878. This is apparently the only reference to a "lectotype" of this species, and, although it was not clearly stated, I assume that this was an attempt to designate ZSZM H 398 as the lectotype of *S. typus*. This attempt was apparently based on the lack of a definite statement by Bleeker (1878) as to the number of specimens he referred to in preparing his original description. In a few places in the original description of *S. typus* it appears as if Bleeker had more than one specimen at hand, but at the end of the description he gave the length of the described specimen ("Longitudo speciminis descripti") as 151‴ (which apparently means 151 mm. total length). In view of his mentioning the length of the described specimen, I think that Bleeker based his description on only one specimen. This position is supported by the facts that the Hamburg specimen (ZSZM H 398) appears to be almost equal in total length (147 + mm.) to Bleeker's specimen and it is the only type specimen of *S. typus* known. I regard this specimen (ZSZM H 398) as the holotype of *S. typus*.

SYNONYMY

Bleeker published two descriptions and two illustrations of *Symphysanodon typus* (1878: 61, pl. 3, fig. 1, and 1880: 28, pl. 5, fig. 2). The descriptions are apparently of the same material. The illustrations, although not identical, are so similar that one may be a copy of the other, and each is a good likeness of the holotype of *S. typus* (ZSZM H 398).

I examined the holotype of *S. typus* (ZSZM H 398), the two syntypes of *Propoma roseum* (BMNH 1879.5.14.164–5), and the holotype of *Rhyacanthias carlsmithi* (USNM 84099), and found that they are conspecific.

Günther (1880) did not clearly indicate the number of specimens upon which he based his original description of *P. roseum*. In two instances he presented body proportions in a manner implying that he had two specimens, whereas he later stated "Length of specimen, 5½ inches." Because the two syntypes of *P. roseum* are almost the same length (105 and 107 mm. SL; at least 5½ inches total length), length cannot be used as a criterion for determining which was intended when Günther gave length of specimen. He described the spine at the angle of the preopercle as flat and projecting. The syntype of 107 mm. SL has a spine at the angle of the left preopercle similar to that described by Günther, but the one of 105 mm. SL lacks a projecting spine at the angle of either preopercle. Except for the caudal fin, the specimen of 107 mm. SL is in better condition than the one of 105 mm. SL. I, therefore, designate as the lectotype of *Propoma roseum* the specimen of 107 mm. SL, which retains BMNH 1879.5.14.164–5; the paralectotype, the specimen of 105 mm. SL, has been assigned a new catalog number (BMNH 1968.8.1.2).

SEXUAL DIMORPHISM

External sexual dimorphism has not been reported for *Symphysanodon typus* and did not exist in the specimens of this species that I examined.

COMPARISONS

Symphysanodon typus may be separated from both *S. octoactinus* and *S. katayamai* by its more slender body, from *S. katayamai* by its shorter depressed anal fin, from *S. maunaloæ* by its possession of more pored scales in the lateral line, and from *S. berryi* by its usual possession of more pored scales in the lateral line and by differences in certain body proportions (see keys). The relation of numbers of total gill rakers on the anterior gill arch to pored lateral-line scales may be used to separate specimens of *S. typus* from those of the other species of the genus (table 1).

DISTRIBUTION

I examined specimens of *Symphysanodon typus* from all of its known localities of capture: New Guinea, Kai Islands, Philippine Islands, and Hawaii. Depth data are available for only two collections—65 fath. (119 m.) off the Philippine Islands and apparently 129 fath. (236 m.) off Kai Islands. Gosline and Brock (1960) stated that *S. typus* ". . . apparently lives well offshore . . ." and that it ". . . has never been seen in the market and has been recorded from Hawaii only on the basis of specimens killed by lava flows." *S. typus* is known from Hawaii only from specimens killed by lava flows. (Gosline, Brock, Moore, and Yamaguchi, 1954, discussed the fish kill resulting from the 1950 eruption of Mauna Loa.)

MATERIAL EXAMINED

I examined 12 specimens, 50 to 165 mm. SL.

Holotype

ZSZM H 398 (112 mm. SL), New Guinea.

Other Material

BMNH 1879.5.14.164–5 (1 specimen, 107 mm. SL; herein designated as the lectotype of *Propoma roseum*), off Kai Islands, *Challenger* station 192.[5] ..... BMNH 1968.8.1.2 (1, 105; the paralectotype of *P. roseum*) from same station as lectotype of *P. roseum*. ..... BMNH 1890.2.26.30 (1, 106), off Kai Islands?, locality of capture not definitely known, but probably from same locality (or general area) as the type specimens of *P. roseum*. ..... UW 12413 (6, 50–80), off the coast of Cavite Province, Luzon, in the south entrance to Manila Bay, Philippine Islands, 65 fath. (119 m.), by beam trawl, October 2, 1948. ..... USNM 84099 (1, ca. 148; holotype of *Rhyacanthias carlsmithi*), off a lava flow from Mauna Loa, Alika, Kau District, Hawaii, by Tom Reinhardt, October 1919 (probably October 6). ..... UH uncataloged (1, 165), picked up off lava flow, Kona, Hawaii, FWS vessel *Henry O'Malley*, June 3, 1950.

[5] Günther (1880) gave the following for *Challenger* station 192: off Kai Islands, 129 fath. Tizard, Moseley, Buchanan, and Murray (1885: 556) stated "The two trawlings, taken in 129 to 140 fathoms (Station 192). . ." and on p. 1012 (op. cit.) gave the data for *Challenger* station 192 as lat. 5° 49′ 15″ S., long. 132° 14′15″ E., 140 fath., September 26, 1874. According to U.S. Naval Oceanographic Office chart H.O. 5592, this position is in the Kai Islands—ca. 7 nautical miles SE. of Taam and ca. 13 nautical miles NW. of Kai Tanimbar.

SYMPHYSANODON KATAYAMAI NEW SPECIES

Figure 2; tables 1 to 4

Symphysanodon typus (non Bleeker, 1878), Kamohara and Katayama, 1959: 2, fig. 2 (synonymy in part of *S. typus* and in part of *S. maunaloæ;* description and illustration representing *S. katayamai* from Japan; distribution referring in part to *S. typus,* in part to *S. maunaloæ,* and in part to *S. katayamai*). ..... Katayama, 1960: 168, pl. 86 (synonymy referring in part to *S. typus,* in part to *S. maunaloæ,* and in part to *S. katayamai;* description and illustration representing *S. katayamai;* distribution referring in part to *S. typus,* in part to *S. maunaloæ,* and in part to *S. katayamai*). ..... Anderson, 1967: 2, 11 (compiled meristic data referring in part to *S. typus,* in part to *S. maunaloæ,* and in

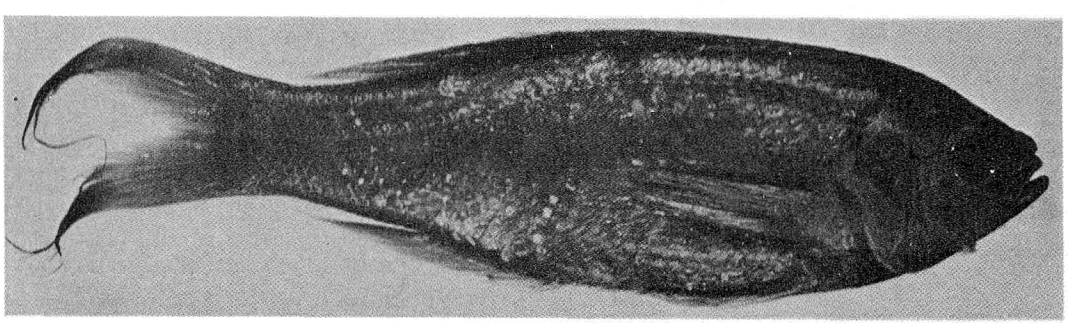

FIGURE 2.—Holotype of *Symphysanodon katayamai* (ZIKU 8206), 163 mm. SL.

part to *S. katayamai;* distribution referring in part to *S. typus*, in part to *S. maunaloæ*, and in part to *S. katayamai*). ..... Katayama, 1968: 105, figs. 1 to 5 (comments on osteology and systematic position).

DIAGNOSIS

Body relatively deep, the depth about 31 percent SL. First pelvic soft ray only slightly produced, not extending to anal fin. Anal fin longer than in other species of *Symphysanodon*, length of depressed anal fin about 39 percent SL. Caudal fin deeply forked, both lobes produced into filaments. Anal soft rays 7. Gill rakers 11 + 24—total 35. Pored lateral-line scales 50.

DESCRIPTION OF THE HOLOTYPE

Maxillary extending posteriorly to beneath posterior part of eye. Length of upper jaw contained in length of mandible 1.00 time. Dorsal profile convex, curving gently to above posterior portion of eye, and rather steeply from this point forward to tip of snout; a slight concavity above nostril region; interorbital region convex; ventral profile convex. Small teeth present in an elliptical patch on vomer and in narrow bands on palatines and ectopterygoids, no teeth apparent on mesopterygoids. Vertical limb of preopercle smooth except for a few small serrae; horizontal limb of preopercle smooth; angle of preopercle slightly produced posteriorly—possibly the remnant of a spine or spinelike process. Anterior part of snout with scales; a single scale present in midline of anterior part of gular region, remainder of gular region without scales; no scales apparent on branchiostegal membranes.

Counts

The following counts are repeated in tables 2, 3, and 4. Dorsal-fin rays IX, 10. Anal-fin rays III, 7. Pectoral-fin rays 16. Gill rakers 11 + 24 —total 35. Pored lateral-line scales 50. Sum of total number of gill rakers on anterior gill arch plus number of pored lateral-line scales 85.

Measurements

Selected measurements are presented in percentage of standard length. Length of head 27.2. Depth of head 21.8. Length of snout 7.3. Horizontal diameter of fleshy orbit 7.4. Width of suborbital 1.3. Height of cheek 7.3. Length of upper jaw 13.5. Length of mandible 13.6. Width of bony interorbital 8.1. Depth of body 31.1. Least depth of caudal peduncle 14.0. Pectoral fin reaching a vertical through base of first dorsal soft ray; length of longer pectoral fin 28.2. Pelvic fin reaching anterior portion of vent; first pelvic soft ray not greatly produced. Length of longer pelvic fin 26.6. Length of base of anal fin 18.1. Length of depressed anal fin 38.9. Lengths of dorsal spines: first 6.2, second 9.4, third—damaged, fourth—damaged, longest (sixth) 13.0, last—damaged. Lengths of anal spines: first >5.5—tip broken, second 9.8, third >10.5—tip broken. Caudal fin deeply forked, both lobes produced into filaments; filaments not produced to the extent of those on some large males of *S. berryi*. Length of upper lobe of caudal fin ca. 58.0. Length of lower lobe of caudal fin ca. 56.0.

Coloration

Kamohara and Katayama (1959, under *S. typus*) described the coloration of this species in Formalin[6] (presumably shortly after capture) as "reddish, a broad longitudinal orange band on the side of body; dorsal yellowish; tip of each lobe of caudal yellowish."

After more than 10 years in Formalin the holotype has faded to a light straw color without any distinctive concentrations of pigment.

OTHER SPECIMENS AND OTHER DESCRIPTIONS

Kamohara and Katayama (1959) described three specimens, 164 to 181 mm. (presumably SL), from Kashiwajima, Kochi Prefecture, Japan, under the name *Symphysanodon typus* Bleeker, 1878. Katayama (1960) repeated (with slight variation) the description given by Kamohara and Katayama. One of the three specimens (ZIKU 8206) mentioned by Kamohara and Katayama (1959) is described herein as the holotype of *Symphysanodon katayamai*. In most respects the earlier descriptions of Japanese *Symphysanodon* agree with the holotype of *S. katayamai*, and in all but two of the meristic characters (numbers of pectoral-fin rays and gill rakers) the count given in the earlier descriptions is identical with that of the holotype. (Pectoral-fin rays were given as 16 or 17, the holotype has 16; gill

[6] The use of trade names in this publication does not imply endorsement of commercial products.

rakers as 11 or 12 + 22 or 23, total 33 to 35, the holotype has 11 + 24, total 35.)

Another of the specimens (YU uncataloged) mentioned by Kamohara and Katayama (1959) was made available to me on loan. This is the specimen on which Katayama (1968) based an osteological study. Because it had been dissected, little of its external morphology could be studied. However, in its extant characters it appears to be conspecific with the holotype of *S. katayamai* (ZIKU 8206). Katayama reported small teeth on the mesopterygoid of this specimen (YU uncataloged). I did not see teeth on the mesopterygoids of the holotype (ZIKU 8206), and the skull was missing from the dissected specimen. Katayama (1968) recorded the number of vertebrae in the dissected specimen as 11 + 14 = 25. My count of the vertebrae from a radiograph of the same specimen is 10 + 15 = 25. This discrepancy is due to differences in determining which vertebra is the first caudal vertebra. (I considered the most anterior vertebra possessing a hemal spine associated with pterygiophores of the anal fin as the first caudal vertebra.)

The third specimen mentioned by Kamohara and Katayama is in the collections of the Zoological Institute, Kochi University (Kochi, Japan). Although I have not seen this specimen, I presume it to be a representative of *S. katayamai.*

SEXUAL DIMORPHISM

Sexual dimorphism is unknown in *Symphysanodon katayamai.*

COMPARISONS

Symphysanodon katayamai may be readily distinguished from other species of the genus by its longer depressed anal fin. The relation of numbers of total gill rakers on the anterior gill arch to pored lateral-line scales may be used to separate *S. katayamai* from all other species of *Symphysanodon* except *S. berryi* (table 1).

DISTRIBUTION

Symphysanodon katayamai is known only from off Kashiwajima, Kochi Prefecture, Japan. No data on the depths inhabited by this species are available.

ETYMOLOGY

This species is named for Masao Katayama, Yamaguchi University, Yamaguchi City, Japan, who made it possible for me to examine specimens of *Symphysanodon* from Japan.

MATERIAL EXAMINED

Holotype

ZIKU 8206 (163 mm. SL), collected off Kashiwajima, Kochi Prefecture, Japan, by S. Noda, K. Amaoka, and T. Hirata, October 15, 1957.

Other Material, Not Considered as Type Material

YU uncataloged (one dissected specimen), data the same as those for holotype. Because this specimen was extensively dissected, I do not consider it a type specimen.

SYMPHYSANODON MAUNALOAE NEW SPECIES

Figure 3; tables 1 to 4

Rhyacanthias species, Jordan, 1921: 648–649, fig. 4 (description of a small specimen, 3⅔ inches in total [?] length, assumed to be the young of *Rhyacanthias carlsmithi;* comments on three other specimens, 2½ to 4 inches in total [?] length, referred with doubt to *R. carlsmithi;* illustration, labeled as *Rhyacanthias carlsmithi* (young), presumably of one of the aforementioned specimens; killed by lava flow from Mauna Loa off Alika, Kau District, Hawaii).

Symphysanodon typus (non Bleeker, 1878), Fowler, 1928: 186 (synonymy of *S. typus;* description of a small specimen, 58 mm. total [?] length, from Alika, Kau District, Hawaii, erroneously considered as a paratype of *Rhyacanthias carlsmithi*). ..... Weber and de Beaufort, 1936: 309, fig. 65 (synonymy referring in part to *S. typus* and in part to *S. maunaloæ,* compiled description [probably representing *S. typus*], illustration [of *Propoma roseum* (= *S. typus*) after Günther, 1880], and distribution referring to *S. typus* and in part to *S. maunaloæ*). ..... Gosline and Brock, 1960: 183–184, 327 (probably in part; partial synonymy of *S. typus;* characters which can be used to identify *Symphysanodon;* Hawaii). ..... Anderson, 1967: 2, 11 (compiled meristic data referring in part to *S. typus,* in part to

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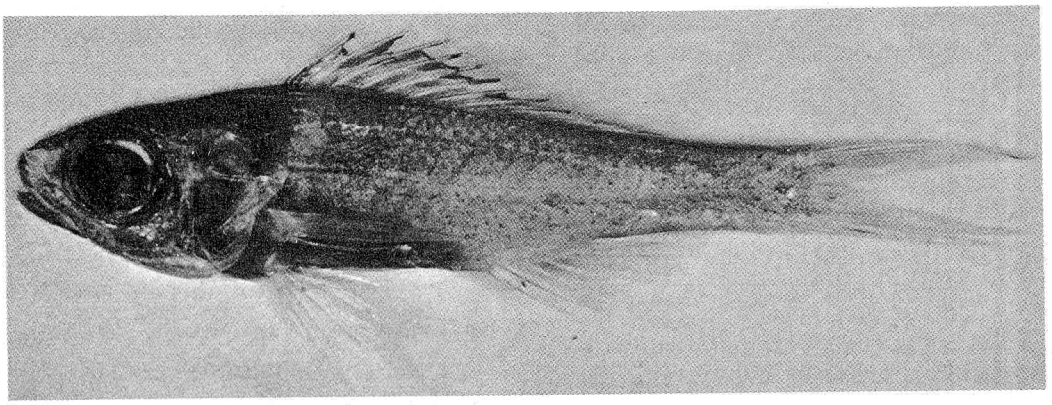

FIGURE 3.—Holotype of *Symphysanodon maunaloae* (USNM 204389, formerly HBL uncataloged), 69 mm. SL.

S. maunaloæ, and in part to *S. katayamai;* distribution referring in part to *S. typus*, in part to *S. maunaloæ*, and in part to *S. katayamai*).

DIAGNOSIS

Body slender, the depth 21.3 to 25.8 percent SL. First pelvic soft ray well produced in a few specimens, but only slightly produced in most (not extending to anal fin). Anal fin short, length of depressed anal fin ca. 24.0 to 29.2 percent SL. Caudal fin deeply forked, both lobes produced, but apparently never produced into excessively long filaments. Anal soft rays 7. Gill rakers 9 to 11 + 22 to 26—total 31 to 37. Pored lateral-line scales 43 to 47.

DESCRIPTION

Maxillary extending posteriorly to about middle of eye or a little beyond. Length of upper jaw contained in length of mandible 0.93 to 1.09 times. Interorbital region flattened. No teeth apparent on vomer, palatines, or pterygoids. Small serrae on vertical limb of preopercle, horizontal limb almost smooth or with a few serrae, mainly near angle; a spine or spinelike process at angle (spine or spinelike process often serrate). No scales on anteriormost part of snout; apparently a few scales in midline of anterior part of gular region in a specimen of 51 mm. SL (no other indications of scales in gular region of this specimen), scales not apparent in gular region of other specimens; frequently one to several scales present on membrane between the third and fourth branchiostegal rays, no other scales apparent on branchiostegal membranes.

Counts

Frequency distributions for the following counts are given in tables 2, 3, and 4. Dorsal-fin rays IX, 10 (IX, 9 on three specimens). Anal-fin rays III, 7. Pectoral-fin rays 15 to 17. Gill rakers 9 to 11 + 22 to 26—total 31 to 37. Pored lateral-line scales 43 to 47. Sum of total number of gill rakers on anterior gill arch plus number of pored lateral-line scales of individual specimens 76 to 81, 83.

Measurements

Ranges of selected measurements are presented in percentage of standard length followed by the value for the holotype of *S. maunaloæ* in parentheses. Length of head 32.0 to 35.6 (34.0). Depth of head 19.5 to 24.0 (21.0). Length of snout 6.4 to 8.2 (7.3). Horizontal diameter of fleshy orbit 10.3 to 14.0 (ca. 12.8). Width of suborbital ca. 0.6 to 1.0 (0.6). Height of cheek 3.8 to 5.6 (4.2). Length of upper jaw 12.5 to 15.1 (14.7). Length of mandible 12.5 to 15.7 (14.5). Width of bony interorbital 7.3 to 9.3 (8.3). Depth of body 21.3 to 25.8 (23.7). Least depth of caudal peduncle 9.6 to 11.9 (10.5). Pectoral fin usually reaching a vertical through base of first or second dorsal soft ray; length of longer pectoral fin 24.3 to 28.1 (26.1). Pelvic fin usually not extending to anal fin, but the first pelvic soft ray produced at least as far as middle of anal fin in several speci-

mens (the medial branch of the first pelvic soft ray reaching approximately to the distal end of the depressed anal fin in three specimens). Length of longer pelvic fin ca. 21.9 to >54 (>40). Length of base of anal fin 13.5 to 16.1 (14.4). Length of depressed anal fin ca. 24.0 to 29.2 (26.7). Lengths of dorsal spines: first 4.3 to 7.3 (6.2), second 10.2 to 13.6 (13.2), third 13.6 to 17.4 (16.5), fourth 15.8 to 18.7 (17.7), longest dorsal spine the fourth on all specimens examined, last 10.7 to 14.5 (14.1). Lengths of anal spines: first 4.0 to 5.5 (5.1), second 10.7 to 14.6 (13.1), third 12.7 to 15.6 (14.8). Caudal fin deeply forked, both lobes produced, but apparently never produced into excessively long filaments. Length of upper lobe of caudal fin ca. 31.2 to ca. 48.9 (39.0). Length of lower lobe of caudal fin ca. 30.0 to ca. 43.1 (>30).

Coloration

Paul J. Struhsaker (personal communication, July 1969) made the following observations on specimens of *S. maunaloæ* collected during *Townsend Cromwell* cruise 35 at station 12 "light reddish over upper parts and caudal; iris pink; darkish vertical bar just behind operculum and above pectoral; also dark bar between eyes."

Jordan (1921) wrote concerning one specimen (designated as *"Rhyacanthias,* species") "Color plain, probably red in life" and later concerning three other specimens (of *"Rhyacanthias,* species") ". . . the back is quite dark in color, made so by a multitude of dark punctulations; the upper fins and caudal also dusky, scales on opercle with a dusky area at base."

Specimens in alcohol have dark punctulations scattered profusely over body (pigment more heavily concentrated dorsally than ventrally). Most individuals are more heavily pigmented in an area which extends for a few scale rows above and below the anteriormost lateral-line scales. Larger, darker flecks of pigment are usually present in irregular rows on sides of body and in two rows on dorsal surface of body anterior and posterior to dorsal fin. The dorsal fin usually has considerable pigment distally; both lobes of caudal fin usually pigmented; other fins mostly pale.

SYNONYMY

Jordan (1921) in a separate section after his description of *Rhyacanthias carlsmithi* described —under the heading *"Rhyacanthias,* species"— a small specimen of 3⅓ inches (ca. 93 mm.) total [?] length, which he assumed to be the young of *R. carlsmithi.* Because Jordan gave the lateral-line scale count as 47—"as nearly as can be counted," this specimen is probably one of *S. maunaloæ.*

Jordan (1921) mentioned three other specimens (under the heading *"Rhyacanthias,* species"), 2½ to 4 inches (ca. 64–ca. 102 mm.) in total [?] length, which he referred with doubt to *R. carlsmithi.* There are three specimens of *Symphysanodon* in the U.S. National Museum (USNM 84101), ca. 42 to ca. 63 mm. SL, from Hawaii that have been labeled as paratypes of *R. carlsmithi.* Because Jordan designated no paratypes and gave no indication that he considered any specimen as a paratype of *R. carlsmithi,* these are not paratypes, but are probably three of the specimens Jordan (1921) mentioned under *"Rhyacanthias,* species." These specimens (USNM 84101) are in such poor condition that it is difficult to identify them to species; however, on the basis of numbers of gill rakers they probably are specimens of *S. maunaloæ.*

Fowler (1928) described a specimen, 58 mm. total [?] length, from the Bishop Museum (no catalog number given) under *Symphysanodon typus* and erroneously stated that it was a paratype of *Rhyacanthias carlsmithi.* I examined a specimen (ca. 49 mm. SL, 54 + mm. total length) of *Symphysanodon maunaloæ* from the Bishop Museum (BPBM 3982), presumably the specimen described by Fowler, and probably one of the specimens Jordan (1921) mentioned under *"Rhyacanthias,* species."

Jordan (1921) gave the catalog number of the specimen of *Rhyacanthias* of 3⅓ inches (see above) as USNM 24101, but gave no reference to a collection for the three specimens of 2½ to 4 inches. The reference to USNM 24101 is in error (the USNM catalog lists 24101 as *Hemilepidotus* sp. from Alaska); USNM 84101 must have been intended. Because the three specimens at the U.S. National Museum and the one at the Bishop Museum were collected by the same individual at apparently the same time and locality as that of the holotype of *Rhyacanthias carlsmithi,* they are with the greatest likelihood the

four small specimens referred to by Jordan (1921) under "*Rhyacanthias*, species."

SEXUAL DIMORPHISM

Seven specimens of *Symphysanodon maunaloæ* (62–86 mm. SL) have the pelvic fin well produced (with the medial branch of first pelvic soft ray reaching anterior part of base of anal fin or beyond), whereas in the other specimens (47–86 mm. SL) the pelvic fin, although usually produced, falls short of the anal fin. I attempted to determine the sex of several individuals, but, because of the relatively small size of the specimens, had only limited success. It seems, however, that the well-produced pelvic fin is a male characteristic (as it is in *S. berryi*).

COMPARISONS

Symphysanodon maunaloæ is easily distinguished from *S. katayamai* and *S. octoactinus* by its more slender body, from *S. katayamai* by its shorter depressed anal fin, and from *S. typus* and *S. berryi* by its possession of fewer pored scales in the lateral line. In addition, the relation of numbers of total gill rakers on the anterior gill arch to pored lateral-line scales may be used to separate specimens of *S. maunaloæ* from specimens of the other species of *Symphysanodon* (table 1).

DISTRIBUTION

Symphysanodon maunaloæ has been collected only off the Hawaiian Islands. The only information available on the depths inhabited by *S. maunaloæ* is from one trawl-station off the northeastern coast of the island of Hawaii (average depth to bottom at this station 130 fath. (238 m.)) and one off the southern coast of Lanai (122 fath. (223 m.)). The other collections of this species were made off lava flows from Mauna Loa. (Gosline, Brock, Moore, and Yamaguchi (1954) discussed the fish kill resulting from the 1950 eruption of Mauna Loa.)

ETYMOLOGY

This species is named for the active volcano Mauna Loa.

MATERIAL EXAMINED

I examined 30 specimens, ca. 42 to ca. 86 mm. SL.

Holotype

USNM 204389, formerly HBL uncataloged, (69 mm. SL), off northeastern coast of island of Hawaii, trawl set: lat. 20°07′ N., long. 155°25′ W., trawl hauled in: lat. 20°08′ N., long. 155°28′ W., average depth to bottom 130 fath. (238 m.), *Townsend Cromwell* cruise 35, station 12, March 31, 1968.

Paratypes

15 specimens, 62 to 86 mm. SL, from same station as holotype, formerly HBL uncataloged; USNM 204388 (12, 63–86) and BPBM 9779 (3, 62–86). ..... BPBM 9778, formerly HBL uncataloged, (1, 84), off southern coast of Lanai in Kealaikahiki Channel, Hawaiian Islands, lat. 20° 43′ N., long. 156° 49′ W., 122 fath. (223 m.), *Townsend Cromwell* cruise 33, station 25, November 4, 1967. ..... UH uncataloged (9, 47–62), collected off lava flow from Mauna Loa, Kona, Hawaii, by Gosline, Hayes, Keen, and Ellis, June 7, 1950. A total of 25 paratypes, 47 to 86 mm. SL.

Other Material, Not Part of the Type Series

BPBM 3982 (1, ca. 49), Alika, Kau District, Hawaii, by Tom Reinhardt, October 1919 (probably October 6). ..... USNM 84101 (3, ca. 42–ca. 63), off lava flow from Mauna Loa, Hawaii, collected by Tom Reinhardt, October 1919 (probably October 6). These specimens (BPBM 3982 and USNM 84101) were in poor condition and not considered during the preparation of the description of the species.

SYMPHYSANODON BERRYI NEW SPECIES

Figure 4; tables 1 to 4

DIAGNOSIS

Body slender, the depth 22.3 to 28.2 percent SL. First pelvic soft ray noticeably produced in males more than ca. 85 mm. SL, extremely filamentous in large males. Anal fin short, length of depressed anal fin 22.8 to ca. 27.6 percent SL. Caudal fin deeply forked, the upper and lower lobes produced into long filaments in large males. Anal soft rays 7. Gill rakers 9 to 12 + 24 to 28—total 34 to 39. Pored lateral-line scales 48 to 52.

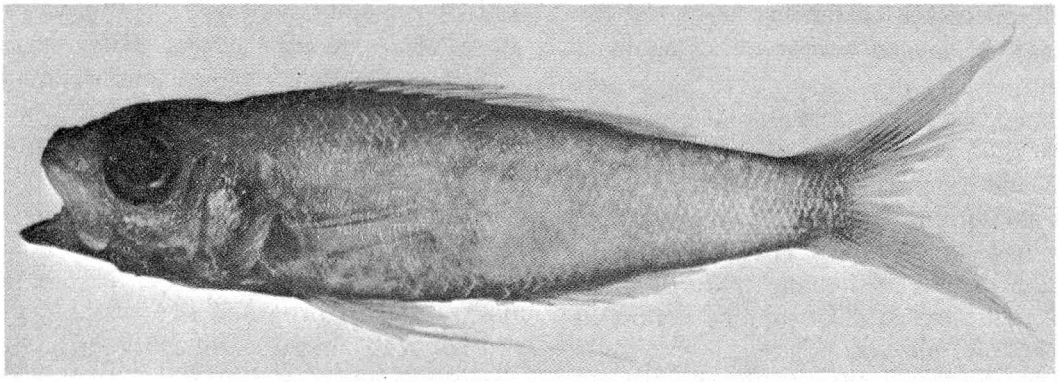

FIGURE 4.—Holotype of *Symphysanodon berryi* (USNM 204086), a male, 115 mm. SL.

DESCRIPTION

Maxillary usually extending posteriorly to beyond middle of eye. Length of upper jaw contained in length of mandible 0.92 to 1.00 time. Interorbital region flattened. No teeth apparent on vomer, palatines, and pterygoids. Dentition better developed and coarser in males than in females. Serrae on vertical limb of preopercle usually well developed; horizontal limb with fewer serrae (mostly near angle) or sometimes almost smooth; usually a single spine (most frequently serrate, often bifid) or spinelike process at angle. Anterior part of snout without scales; scales usually absent (or at least not apparent) on gular region and branchiostegal membranes; on a very few specimens a number of scales present in mid-line of anterior part of gular region, on some others extremely small scales may be embedded in this region; a few specimens with a scale (rarely two) on membrane between third and fourth branchiostegal rays (rarely on membrane covering the third or fourth branchiostegal ray).

Counts

Frequency distributions for the following counts are given in tables 2, 3, and 4. Dorsal-fin rays IX, 10 (VIII, 11 on one specimen and IX, 9 on one). Anal-fin rays III, 7. Pectoral-fin rays 16 to 18. Gill rakers 9 to 12 + 24 to 28—total 34 to 39. Pored lateral-line scales 48 to 52. Sum of total number of gill rakers on anterior gill arch plus number of pored lateral-line scales of individual specimens 83 to 90.

Measurements

Ranges of selected measurements are presented in percentage of standard length followed by the value for the holotype of *S. berryi* in parentheses. Length of head 30.7 to 36.0 (32.8). Depth of head 20.1 to 23.3 (23.1). Length of snout 6.2 to 8.9 (8.9). Horizontal diameter of fleshy orbit 10.0 to 13.2 (10.0). Width of suborbital 0.8 to 1.2 (1.1). Height of cheek 4.4 to 6.4 (5.7). Length of upper jaw 14.0 to 16.5 (14.6). Length of mandible 13.6 to 15.9 (14.2). Width of bony interorbital 7.2 to 9.0 (8.0). Depth of body 22.3 to 28.2 (26.1). Least depth of caudal peduncle 9.5 to 11.8 (11.6). Pectoral fin usually reaching a vertical through base of first or second dorsal soft ray; length of longer pectoral fin 23.7 to 27.2 (24.4). Pelvic fin usually not extending to vent in females; first pelvic soft ray noticeably produced in males more than ca. 85 mm. SL, increasing in length with increase in SL, extremely filamentous in large specimens; medial branch of first pelvic soft ray reaching past fork of caudal fin in some large males. Length of longer pelvic fin ca. 20.3 to >87 (ca. 54), varying in females from ca. 21.2 to 24.5 and in males from ca. 30.0 to >87 in specimens more than ca. 85 mm. SL. Length of base of anal fin 12.7 to 15.8 (14.9). Length of depressed anal fin 22.8 to ca. 27.6 (25.1). Lengths of dorsal spines: first 5.5 to 7.5 (6.7), second 10.1 to 12.3 (11.4), third 14.0 to 16.5 (15.4), fourth 16.0 to 18.9 (16.7), longest (fourth, fifth, or sixth—most frequently the fourth or fifth) 16.0 to 18.9 (16.7), last ca. 12.3 to >15.7 (14.2). Lengths of anal spines: first 3.3 to 5.6 (4.3), second 9.9 to 13.4 (11.6), third 11.1 to 15.0 (12.6). Caudal fin deeply forked; the upper and lower lobes produced into fila-

ments in large males (filaments becoming extremely long in largest males), increasing in length with increase in SL. Length of upper lobe of caudal fin ca. 29.4 to >128 (ca. 44), varying from ca. 30.1 to >35 in females more than ca. 80 mm. SL and from ca. 34.3 to >128 in males more than ca. 85 mm. SL. Length of lower lobe of caudal fin ca. 28.0 to >111 (ca. 39), varying from ca. 29.5 to >34 in females more than ca. 80 mm. SL and from ca. 32.4 to >111 in males more than ca. 85 mm. SL.

Values for depth of body, lengths of fins and fin-lobes, length of base of anal fin, and lengths of anal spines are based on measurements of more than 110 specimens; those for all other morphometric characters listed above on measurements of a graded size series.

Coloration

Live coloration is unknown, but a 35-mm. color photograph was taken shortly after capture of a male specimen (TABL 101317, 120 mm. SL) from *Silver Bay* station 5191. Iris silvery, except for a little orange on dorsal curvature, some dull yellow to dark gray on anterior curvature, a little light gray on ventral curvature, and considerable dark gray on posterior curvature. Head mostly bright orange. Body mainly bright orange, except ventrolateral surface of anterior end of body silver with some orange. Area beneath base of dorsal fin red-orange. Dorsal spines and soft rays mostly orange. First interradial membrane of dorsal fin red-orange; a somewhat triangular silvery area on proximal portions of second through sixth interradial membranes; an elliptical orange to red-orange area on proximal portions of seventh through ninth interradial membranes; distal part of membrane of soft dorsal fin dull orange; remainder of dorsal fin mostly dull yellow. Area above base of anal fin bright orange. Anal fin not clearly visible. Pectoral fin orange basally, rest of fin pale to silvery. Pelvic spine and filamentous first pelvic soft ray silvery, rest of pelvic fin orange proximally grading into light orange or pink and then into dull yellow distally. Outer rays (including filamentous ones) of both lobes of caudal fin red-orange; inner two or three rays of each lobe and midcaudal rays dull yellow to silvery distally (i.e., dull yellow to silvery inner area of caudal fin crescent shaped), orange proximally.

A less distinct, 35-mm. color photograph of a smaller specimen presumably from *Silver Bay* station 5191 shows no pronounced differences from the above description except that the fins (particularly the dorsal and pelvic fins) are paler.

A 35-mm. color photograph of a male specimen (TABL 101316, 134 mm. SL) from *Oregon* station 5414 shows some differences from the preceding description. Iris mostly orange. Head and fins much less brightly colored. Dorsolateral surface of body dull orange overlying pale blue. Ventrolateral surface of body mostly silvery with some pale blue on caudal peduncle.

All photographed specimens were collected during daylight. Those from *Silver Bay* station 5191 were photographed in sunlight, the one from *Oregon* station 5414 in artificial light (PROX-O-LITE). It is not known whether the differences in coloration mentioned are real or a result of differences in lighting used in the photography. (Frederick H. Berry and George C. Miller made the photographs, which are deposited in the collection of color slides at TABL.)

Thirty-one days after capture (and shortly after transfer to isopropyl alcohol) notes were made on the color remaining on the three specimens of *S. berryi* (TABL 101315, 92–99 mm. SL) collected by the *Undaunted* off British Honduras. Dorsal part of head with considerable orange on two specimens (females of 92 and 98 mm. SL). Dorsal part of body (particularly above lateral line) with much orange on the female of 98 mm. SL. Membrane of dorsal fin (particularly spiny dorsal) with much dark pigment on all three specimens. Filament of lower caudal lobe red on one specimen (a male of 99 mm. SL). Distal tip of upper caudal lobe with some dark pigment on both female specimens. Distal tip of lower caudal lobe with some dark pigment in female of 92 mm. SL.

In alcohol, specimens greater than ca. 80 to 90 mm. SL are usually a light straw color except for small spots of dark pigment usually arranged in irregular rows along the side of the body and in one or two (usually two) rows on the dorsal surface of the caudal peduncle; heavy

concentrations of smaller spots of dark pigment frequently apparent on opercle and preopercle and usually present in an area which extends for a few scale rows above and below the anteriormost lateral-line scales. Specimens less than ca. 80 to 90 mm. SL show a similar pattern of pigmentation, but usually are more heavily covered with the smaller spots of pigment, particularly on the head and dorsolateral surface of the body. The dorsal fin shows considerable dark pigment on most specimens less than ca. 100 to 110 mm. SL, mostly pale in larger specimens; the caudal fin usually has some dark pigment in specimens less than ca. 80 mm. SL, usually straw colored proximally and pale distally in specimens more than ca. 80 mm. SL; other fins pale. (Pigment spots may be difficult to distinguish on some specimens without magnification.)

PREVIOUS REFERENCE TO *SYMPHYSANODON BERRYI*

In an earlier publication (Anderson, 1967) I presented a key for the identification of two undescribed species of western Atlantic *Symphysanodon*. The species designated as "*Symphysanodon* sp. A" is *S. berryi*.

SEXUAL DIMORPHISM

The sex was determined on 108 specimens (56 males, 73–137 mm. SL, and 52 females, 67–123 mm. SL). The 52 males more than 84 mm. SL and one of 73 mm. SL have the first pelvic soft ray noticeably produced; many males of more than 100 mm. SL have the medial branch of the first pelvic soft ray produced into a long filament which reaches the base of the caudal fin or beyond. Most males of more than 100 mm. SL have the caudal fin lobes produced into long filaments. None of the females have the first pelvic soft ray or caudal fin lobes produced into long filaments. In addition, the dentition is better developed and coarser in males than in females. Two specimens (105 and 125 mm. SL) on which I was unable to determine the sex have the first pelvic soft ray well produced and, thus, may be presumed to be males. The other specimens on which the sex was not determined are small (49–83 mm. SL, most of them less than 70 mm. SL).

Sexual dimorphism was not observed in the other characters studied.

COMPARISONS

Symphysanodon berryi may be separated from *S. octoactinus* and *S. katayamai* by its more slender body and by its shorter depressed anal fin, from *S. maunaloæ* by its possession of more pored scales in the lateral line, and from *S. typus* by its usual possession of fewer pored scales in the lateral line and by differences in certain body proportions (see keys). The relation of numbers of total gill rakers on the anterior gill arch to pored lateral-line scales may be used to separate specimens of *S. berryi* from those of all other species of the genus except *S. katayamai* (table 1). *S. berryi* seems to differ from the other species of *Symphysanodon* (with the apparent exception of *S. maunaloæ*) in exhibiting pronounced sexual dimorphism.

DISTRIBUTION

S. berryi has been collected in the western Atlantic off the Bahamas, Dominican Republic, Puerto Rico, Tobago, Mexico, British Honduras, Honduras, and Nicaragua in 120 to 260 fath. (220–476 m.). Specimens of *S. berryi* were collected at *Pillsbury* station 582. The depth data for this station are 250 to 20 fath. (458–37 m.). According to Thomas H. Fraser (in litt., April 22, 1968), *Pillsbury* station 582 was made going up the slope at Arrowsmith Bank. The vessel turned sharply in about 20 fath. and terminated the tow in about 155 fath. (283 m.). The net probably did not fish as shallow as 20 fath.

One specimen of *S. berryi* was collected in company with one of *S. octoactinus* at *Gerda* station 693 off Grand Bahama Island in 160 to 150 fath. (293–274 m.).

ETYMOLOGY

This species is named for Frederick H. Berry, who first brought it to my attention and who has taught me, stimulated my interest, and encouraged me.

MATERIAL EXAMINED

I examined 136 specimens, 47 to 137 mm. SL.

Holotype

USNM 204086 (a male, 115 mm. SL), off southern coast of Great Inagua Island, Bahamas,

lat. 20°45′ N., long. 73°33′ W., 217 to 200 fath. (397–366 m.), *Oregon* station 5414, May 24, 1965.

Paratypes

43 specimens, 87 to 137 mm. SL, from same station as holotype: AM I. 15402–001 (1 specimen, 122 mm. SL), AMNH 28501 (2, 110–128), ANSP 112724 (2, 112–120), BPBM 7305 (1, 109), BMNH 1969.5.16.2–3 (2, 118–121), BOC 5988 (1, 125), CU 64262 (2, 109–119), IRSNB 474 (1, 133), LACM 30769–1 (2, 115–120), MCZ 46518 (2, 110–135), MNHN 1969–165 (2, 106–111), RMNH 26071 (1, 121), SU 67142 (2, 114–124), TABL 101316 (10, 93–134), TU 57443 (2, 116–120), UF 16425 (2, 112–125), UH uncataloged (1, 114), UMMZ 188888 (2, 92–112), USNM 204087 (3, 88–137), UW 200444 (1, 87), and ZSZM 4201 (1, 118). ..... UMML 2679 (4, 73–93), north of Little Bahama Bank, lat. 27°29′ N., long. 78°58′ W., 200 fath. (366 m.), *Combat* station 236, February 2, 1957. ..... UMML 20774 (1, 74), off southern coast of Grand Bahama Island, lat. 26°34′ N., long. 78°26–25′ W., 160 to 150 fath. (293–274 m.), *Gerda* station 693, July 21, 1965. ..... 26 specimens, 49 to 86 mm. SL, off eastern coast of the Dominican Republic, lat. 18°24′ N., long. 68°05′ W., 200 fath. (366 m.), *Silver Bay* station 5190, October 17, 1963; TABL 101313 (6, 56–83), UMML 15814 (17, 60–78), and USNM 204088 (3, 49–86). ..... 24 specimens, 71 to 120 mm. SL, off western coast of Puerto Rico, lat. 18°26.5′ N., long. 67°41′ W., 260 fath. (476 m.), *Silver Bay* station 5191, October 18, 1963; TABL 101317 (21, 71–120), and USNM 204089 (3, 96–108). ..... FMNH 66922 (1, 54), off the southern coast of Isla de Vieques, Puerto Rico, lat. 18°05′ N., long. 65°21′ W., 120 fath. (220 m.), *Oregon* station 2627, September 29, 1959. ..... 7 specimens, 75 to 102 mm. SL, off western coast of Puerto Rico, lat. 18°03′ N., long. 67°27′ W., 150 to 180 fath. (274–329 m.), *Oregon* station 2643, October 5, 1959; FMNH 66923 (4, 75–100) and UMML 7487 (3, 77–102). ..... UMML 7043 (2, 86–87), off western coast of Puerto Rico, lat. 18°14′ N., long. 67°20′ W., 210 fath. (384 m.), *Oregon* station 2646, October 5, 1959. ..... TABL 106432 (1, 81), off northwestern coast of Tobago, lat. 11°30′ N., long. 60°46′ W., 200 to 240 fath. (366–439 m.), *Oregon* station 5028, September 22, 1964. ..... UMML 23902 (6, 83–96), east of Arrowsmith Bank, off Quintana Roo, Mexico, lat. 21°10′ N., long. 86°18′ W., 250 to 20 fath. (458–37 m.), *Pillsbury* station 582, May 23, 1967. ..... TABL 101315 (3, 92–99), south southwest of Glovers Reef, off British Honduras, lat. 16°35′ N., long. 87°56′ W., 150 to 175 fath. (274–320 m.), *Undaunted* cruise 6703, station 76 (TABL 67–174), May 19, 1967. ..... FMNH 66918 (8, 80–119), off northeastern coast of Honduras, lat. 16°39′ N., long. 82°29′ W., 225 fath. (412 m.), *Oregon* station 1870, August 21, 1957. ..... FMNH 66919 (1, 99), off eastern coast of Nicaragua, lat. 11°31′ N., long. 83°09′ W., 150 fath. (274 m.), *Oregon* station 1903, September 9, 1957. ..... 6 specimens, 75 to 112 mm. SL, off eastern coast of Nicaragua, lat. 11°34′ N., long. 83°07′ W., 125 fath. (229 m.), *Oregon* station 1904, September 9, 1957; FMNH 66920 (5, 75–112) and FMNH 66921 (1, 108). A total of 133 paratypes, 49 to 137 mm. SL.

Other Material, Not Part of the Type Series

UMML 24751 (1, 47), collection data the same as that for UMML 23902. ..... TABL 106275 (1, 87), collection data the same as that for TABL 101317. These specimens (UMML 24751 and TABL 106275) were not considered during the preparation of the description of the species.

SYMPHYSANODON OCTOACTINUS NEW SPECIES

Figure 5; tables 1 to 4

DIAGNOSIS

Body deeper than in other species of *Symphysanodon*, the depth 33.4 to 36.0 percent SL. First pelvic soft ray not greatly produced. Anal fin short, length of depressed anal fin 28.5 to 32.3 percent SL. Caudal fin deeply forked, but the lobes apparently never greatly produced. Anal soft rays 7 or 8 (usually 8). Gill rakers 12 to 14 + 26 to 29—total 39 to 42. Pored lateral-line scales 45 or 46.

DESCRIPTION

Maxillary extending posteriorly to approximately middle of eye or a little beyond. Length

of upper jaw contained in length of mandible 1.04 to 1.13 times. Interorbital region flattened. A band of small toothlike irregularities on palatines of largest specimen (FMNH 66924, 108 mm. SL), teeth not apparent on palatines of other specimens; teeth not apparent on vomer or pterygoids. Preopercle almost smooth or with small serrae (particularly in region of angle); rarely with a spinelike process at angle. Anterior part of snout, most of gular region, and most of branchiostegal membranes without scales; often one to several scales present in midline of anterior part of gular region; frequently one to several scales present on the membrane covering the fourth branchiostegal ray.

Counts

Frequency distributions for the following counts are given in tables 2, 3, and 4. Dorsal-fin rays[7] IX or X, 9 or 10 (usually IX, 10). Anal-fin rays III, 7 or 8 (usually 8). Pectoral-fin rays 16 or 17 (usually 16). Gill rakers 12 to 14 + 26 to 29—total 39 to 42. Pored lateral-line scales 45 or 46. Sum of total number of gill rakers on anterior gill arch plus number of pored lateral-line scales of individual specimens 84, 86, 88.

Measurements

Ranges of selected measurements are presented in percentage of standard length followed by the value for the holotype of *S. octoactinus* in parentheses. Length of head 33.9 to 36.3 (34.6). Depth of head 27.4 to 30.9 (29.0). Length of snout 6.4 to 8.6 (7.6). Horizontal diameter of fleshy orbit 12.1 to 15.4 (14.4). Width of suborbital 0.6 to 1.0 (0.8). Height of cheek 5.6 to 8.0 (7.3). Length of upper jaw 14.4 to 16.5 (16.1). Length of mandible 16.0 to 18.4 (18.0). Width of bony interorbital 9.0 to 10.5 (9.9). Depth of body 33.4 to 36.0 (34.8). Least depth of caudal peduncle 12.0 to 13.2 (12.8). Pectoral fin usually reaching a vertical through base of third or fourth dorsal soft ray; length of longer pectoral fin 28.3 to >30.9 (30.5). Pelvic fin usually reaching anal fin; first pelvic soft ray not greatly produced. Length of longer pelvic fin ca. 25.8 to ca. 27.9 (ca. 25.8). Length of base of anal fin 16.5 to 18.8 (18.4). Length of depressed anal fin 28.5 to 32.3 (30.9). Lengths of dorsal spines: first 6.1 to 7.8 (>6.3), second 10.1 to 11.5 (10.7), third 12.8 to 14.7 (>13.1), fourth 13.8 to 16.5 (>15.6), longest (fifth, sixth, or seventh—most frequently the fifth) 15.4 to 18.4 (16.6), last 14.1 to 16.4 (15.2). Lengths of anal spines: first 7.0 to 9.1 (7.3), second 13.0 to 14.9 (14.4), third 14.9 to 18.0 (16.4). Caudal fin deeply forked, the lobes apparently never greatly produced (however, caudal fin damaged on most specimens). Length of upper lobe of caudal fin ca. 38.6 to >42.0 (ca. 41.4). Length of lower lobe of caudal fin ca. 37.2 to 39.1 (ca. 37.2).

[7] One specimen (UMML 11050, 58 mm. SL) has 10 dorsal spines. The ninth spine in the series appears to be intercalated between what would normally be the last two dorsal spines. It is shorter than either the spine anterior or posterior to it and arises abnormally close to the last spine.

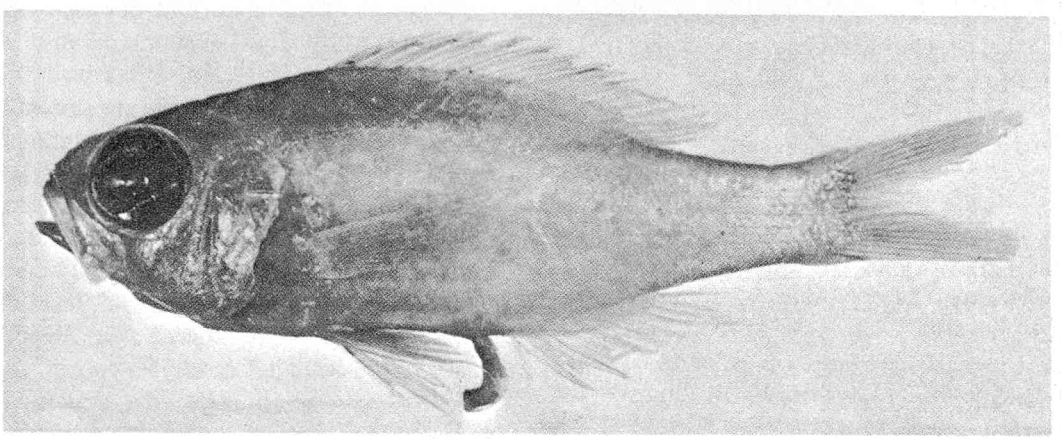

FIGURE 5.—Holotype of *Symphysanodon octoactinus* (USNM 204084, formerly UMML 20775), 79 mm. SL.

Coloration

No information is available on live coloration. In alcohol, specimens are a uniform straw color except for a variable number of small spots of dark pigment scattered over head and body (some larger spots of pigment usually present, mainly above the lateral line). Dorsal fin and proximal part of caudal fin usually have a considerable number of small spots of dark pigment (caudal fin of holotype with a very narrow dusky border distally); other fins mostly pale. (Pigment spots are not easily seen without magnification.)

PREVIOUS REFERENCE TO *SYMPHYSANODON OCTOACTINUS*

The species designated as "*Symphysanodon* sp. B" by Anderson (1967: 12) is *S. octoactinus*.

SEXUAL DIMORPHISM

No external evidence of sexual dimorphism was observed in *S. octoactinus*.

COMPARISONS

Specimens of *Symphysanodon octoactinus* may be readily distinguished from specimens of all other species of the genus by their deeper bodies, by their usual possession of an additional anal soft ray, and by the relation of number of total gill rakers on the anterior gill arch to number of pored lateral-line scales (table 1).

DISTRIBUTION

Symphysanodon octoactinus has been collected in the western Atlantic off the Bahamas, Puerto Rico, Nicaragua, and Panama in 85 to 160 fath. (156–293 m.). The holotype of *S. octoactinus* was caught along with one specimen of *S. berryi* at *Gerda* station 693 off Grand Bahama Island in 160 to 150 fath. (293–274 m.).

ETYMOLOGY

The name *octoactinus*, suggested by Albert Schwartz (Miami Dade Junior College), is from the Greek (octo, eight; actis, ray) and refers to the usual number of anal soft rays (eight) found in this species. This name should be considered as an adjective.

MATERIAL EXAMINED

I examined 19 specimens, 58 to 108 mm. SL.

Holotype

USNM 204084, formerly UMML 20775, (79 mm. SL), off southern coast of Grand Bahama Island, lat. 26°34′ N., long. 78°26–25′ W., 160 to 150 fath. (293–274 m.), *Gerda* station 693, July 21, 1965.

Paratypes

FMNH 66924 (1, 108 mm. SL), off western coast of Puerto Rico, lat. 18°24′ N., long. 67°15′ W., 100 fath. (183 m.), *Oregon* station 2655, October 6, 1959. ..... UMML 12273 (2, 69–85), off eastern coast of Nicaragua, lat. 12°32′ N., long. 82°25′ W., 85 fath. (156 m.), *Oregon* station 3577, May 23, 1962. ..... 15 specimens, 58 to 101 mm. SL, off northern coast of Panama, lat. 09°02′ N., long. 81°26′ W., 100 fath. (183 m.), *Oregon* station 3595, May 30, 1962; ANSP 112723 (1, 75), BMNH 1969.5.16.4 (1, 76), TABL 101314 (2, 69–101), UMML 11050 (8, 58–78), and USNM 204085 (3, 70–82). A total of 18 paratypes, 58 to 108 mm. SL.

ZOOGEOGRAPHY AND PHYLOGENY OF THE GENUS *SYMPHYSANODON*

All of the specimens of *Symphysanodon* known are from the western Pacific, central Pacific, or western Atlantic, and most specimens (155 of 200) are from a relatively small area in the western Atlantic (the Caribbean Sea and off the islands of the West Indies) from which a large number of collections have been made within the last 20 years.

Species of *Symphysanodon* show a marked predilection for moderate depths—65 to 260 fath. (119–476 m.)—around islands. The three Pacific species (*S. typus, S. katayamai*, and *S. maunaloæ*) have been captured exclusively off insular areas, whereas the two western Atlantic species (*S. berryi* and *S. octoactinus*) have been collected off both the Caribbean coast of continental America and off islands in the West Indies. Most of the specimens of *S. berryi* have been collected off islands in the West Indies, but most of those of *S. octoactinus* are from the Caribbean Sea off Central America.

Although depth data for Pacific *Symphysanodon* are meager (only four depth records, none for *S. katayamai*), these species may frequent somewhat shallower waters—65 to 130

fath. (119–238 m.)—than do the Atlantic species—85 to 260 fath. (156–476 m.). Of the Atlantic species, *S. berryi* has been found in deeper waters—120 to 260 fath. (220–476 m.)—than has *S. octoactinus*—85 to 160 fath. (156–293 m.).

When habitats suitable for *Symphysanodon* have been more extensively explored in the Pacific, Indian Ocean, and eastern Atlantic, more secure foundations for developing explanations for the patterns of distribution of the species of the genus will be available. However, from the accessible data, it seems that the genus may have evolved in the central western Pacific and spread northward to colonize the area off Japan and eastward to the Hawaiian Islands. If *Symphysanodon* arose in the western Pacific and spread to the central Pacific, two routes for invading the western Atlantic would have been available—one from the western Pacific via the Indian Ocean and eastern Atlantic and the other from the central Pacific via the eastern Pacific. The route via the eastern Pacific would have been shorter and less encumbered by land as a barrier.

On the basis of our fragmentary knowledge of *Symphysanodon,* it seems that the wide-ranging species, *S. typus,* may resemble the progenitor of the contemporary species of the genus more closely than do any of the other modern species and that some (perhaps all) of the modern species may be derivatives of a *typus*-like ancestor. Descent from a *typus*-like predecessor seems to have been the case for *S. maunaloæ* and perhaps also for *S. katayamai.*

The geographically well-separated species *S. typus* (western and central Pacific) and *S. berryi* (western Atlantic) are the most difficult to separate when morphological characters are used. Their similar morphology might be the result of parallelism (or convergence) within the genus or of slight divergence from a rather recent common ancestor. If *S. typus* and *S. berryi* have diverged comparatively recently, the more likely route for colonization of the western Atlantic by *Symphysanodon* would have been via the eastern Pacific.

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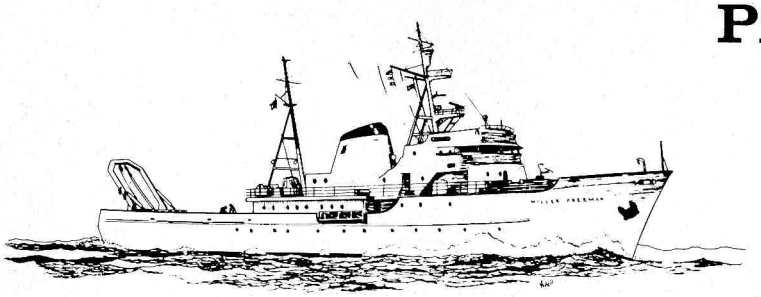

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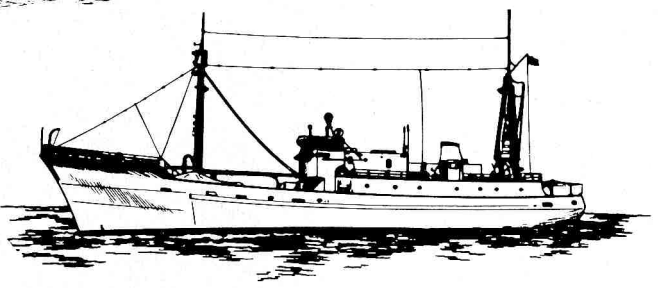

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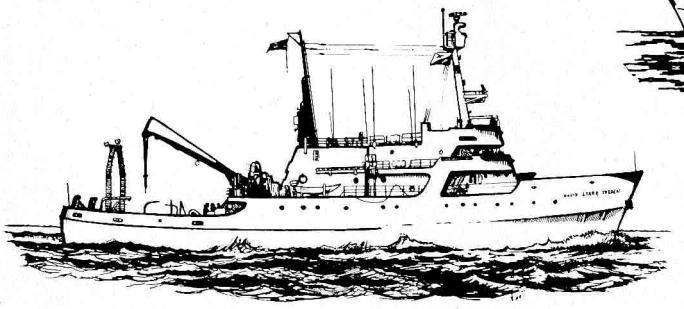

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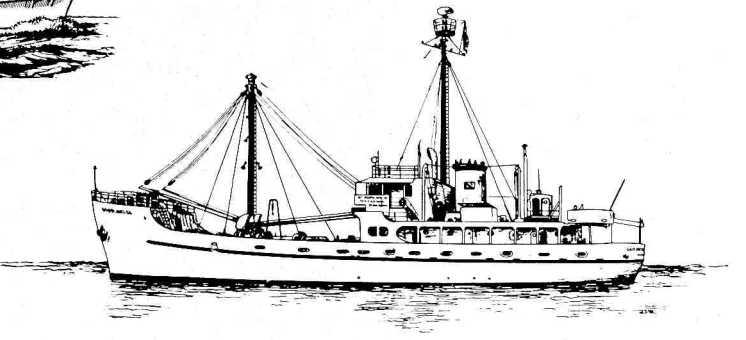

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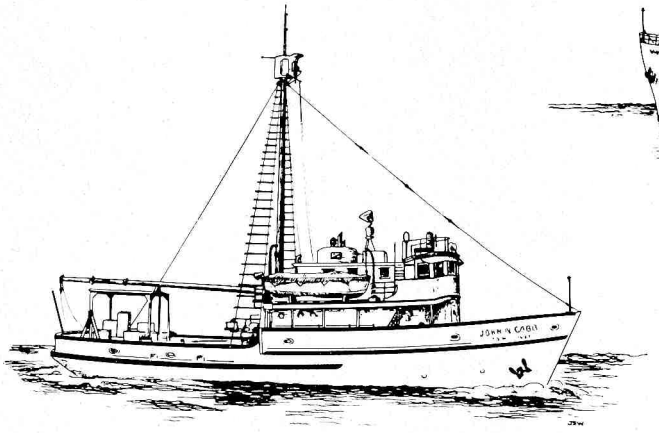

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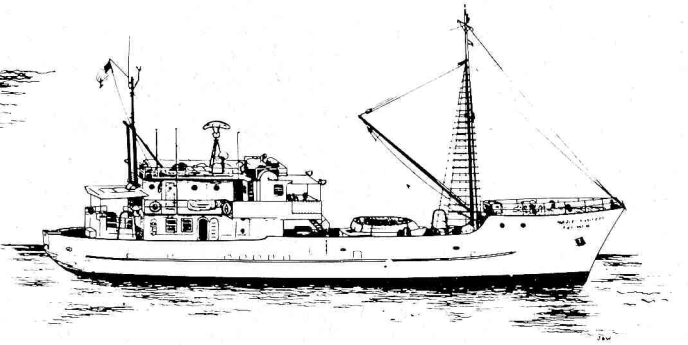

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COPEPODS AND NEEDLEFISHES: A STUDY IN HOST-PARASITE RELATIONSHIPS

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ABSTRACT

A survey of museum material of the species of needlefishes (Belonidae) found 3,863 copepods of 31 species from 25 species of needlefishes. Twelve species of copepods are described as new; one is included in a new genus (*Acusicola*) of Ergasilidae. The new species are: *Ergasilus spatulus, E. argulus, E. coleus, E. semicoleus, E. inflatipes, Acusicola cunula, Paraergasilus remulus, Parabomolochus ensiculus, P. constrictus, P. sinensis, Nothobomolochus digitatus,* and *Colobomatus goodingi.* In addition, 11 previously described species are reported: *Ergasilus orientalis* Yamaguti, *Acusicola tenax* (Roberts), *Parabomolochus bellones* (Burmeister), *Nothobomolochus gibber* (Shiino), *Caligus tylosuri* (Rangnekar), *C. belones* Krøyer, *C. malabaricus* Pillai, *Caligodes laciniatus* (Krøyer), *Lernanthropus belones* Krøyer, *L. tylosuri* Richiardi, and *Lernaeolophus sultanus* (Milne-Edwards). Eight additional species were not named or described in detail because of insufficient material. The copepod fauna of each species of needlefish is listed separately after the taxonomic descriptions of the copepods.

Eight questions regarding needlefishes and their copepod parasites are considered:

(1) Host specificity. The ergasilid and bomolochid copepods show little host specificity; *Caligodes laciniatus, Lernanthropus belones,* and *L. tylosuri* are restricted to certain groups of needlefishes.

(2) Distributions. Maps of the ranges of the common species of copepods and their needlefish hosts show general agreement; however, *Colobomatus goodingi* is restricted to warmer waters than its hosts.

(3) Intraspecific variation in copepods. Total lengths of female *Caligodes laciniatus* and *Lernanthropus belones* were related to host species and geography, respectively. Lengths of setae in *Parabomolochus bellones* also varied geographically rather than by host species.

(4) Relative evolutionary rates. The four worldwide species of needlefishes appear to be more highly differentiated than the four worldwide species of copepods. One widespread copepod, *Parabomolochus bellones,* has given rise to *P. constrictus* in the eastern Pacific, whereas the needlefish hosts have differentiated to only the subspecific level.

(5) Effect of host size. Specialized copepods (those possessing holdfasts) are attached to needlefishes of larger than average size; generalized copepods that lack these adaptations are found on average-sized needlefishes.

(6) Competition between copepods. Individual needlefishes infested with several species of copepods have copepods living in different ecological niches on the host. Distributional evidence indicates that the widespread *Parabomolochus bellones* is being replaced in the Indo-West Pacific by *P. sinensis* and two species of *Nothobomolochus.*

(7) Variation in infestation in time and space. The relative infestation of Bahamian *Strongylura notata* with *Colobomatus goodingi* seems to be increasing. Geographic differences in infestation of widespread hosts were prominent in *Caligodes laciniatus, Lernanthropus tylosuri,* and *Colobomatus goodingi.*

(8) Nature of the symbiotic relationship. The copepods with holdfasts appear to be doing at least mechanical damage to their hosts; the bomolochids appear to be commensal or even mutualistic.

This paper is a cooperative undertaking by a specialist in a parasite group (Cressey) and one in the host group (Collette). Misidentification of host animals has marred most past attempts of parasitologists to analyze collection and literature data. Identifications of hosts have rarely been authoritative because only occasionally has a specialist for the hosts been consulted. We have not used literature records in our analysis because the resulting misidentifications in the literature cloud

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the analysis of host-parasite relations and because our material is so abundant. In this paper we present the results of our survey of the parasitic copepods found on the needlefishes (Belonidae). Cressey is responsible for the identifications and descriptions of the parasitic copepods, and Collette is responsible for the identifications of the hosts and most of the collection data. Both authors are responsible for the interpretations and analysis of data.

We believe a host specialist and a parasite specialist must work together to answer the questions we consider here. Data on host distribution, ecology, and evolution can then be integrated with parasite data. Only in this way can we solve some of the important problems concerning the biology and evolution of host and parasite.

We have considered the following questions about needlefishes and their copepod parasites:

1. To what extent are copepods host-specific?
2. How do the distributions of hosts and parasites compare?
3. Is intraspecific variation in copepods related to host influence, ecology, or geography?
4. What are the relative rates of evolution of host and parasite?
5. Do larger host individuals have a greater copepod fauna?
6. Is there competition among different species of parasites on the same hosts?
7. How do the relative infestations of a given host species by a given copepod species compare in time and space? (We use the word infestation as the appropriate term for an ectoparasite or commensal that is a nonmultiplying invader as opposed to a multiplying one.)
8. Are the copepods associated with needlefishes parasitic in the strict sense or are some of them commensal or mutualistic?

This paper consists of three major parts: first, a taxonomic description of copepods found on needlefishes; second, an account of the copepods we found on each species of needlefish; and third, a consideration of the questions posed above on the basis of the data presented in the first two sections.

We have not subjected our data to sophisticated statistical tests for several reasons. The needlefish material available in museum collections is strongly biased as regards such things as locality, number of specimens, and dates of collection. Then a further bias has been introduced by selecting certain needlefishes to examine. Ideally, one should plan a sampling program for needlefishes in time and space and then subsample the hosts, especially with regard to size. But we have used historic collections (or accumulations) so we believe it is preferable to present tabular summaries or graphs of what we found and then to try to explain the results. Our use of museum collections of needlefishes has certainly biased our results in one other respect—because many external forms are not firmly attached we have found far fewer external copepod parasites (such as *Caligus*) than we would have found on fresh material.

MATERIALS AND METHODS

The 28 species of epipelagic fishes composing the needlefish family Belonidae are found in fresh waters, estuaries, and marine habitats both inshore and offshore. Four species are worldwide; the other 24 species have more restricted distributions. Needlefishes vary in maximum body length from 42 mm. for the two neotenic South American fresh water species of *Belonion* to 950 mm. for the worldwide *Tylosurus acus*. While preparing a monograph on the Belonidae, Collette looked for copepods on 2,720 needlefishes from more than 800 collections. Copepods were found on all but three species—the rare South African *Petalichthys capensis*, of which only a single specimen was examined, and the two species of *Belonion*. The nomenclature used for the needlefishes in this paper is based on Collette and Berry (1965), Parin (1967), and Collette and Parin (1970).

The needlefishes examined for copepods are housed in most of the major fish collections in the world. Abbreviations of these collections are listed below. Full data on each host collection are not included in this paper but are available from Collette:

AMNH: American Museum of Natural History, New York, N.Y.
ANSP: Academy of Natural Sciences, Philadelphia, Pa.
BMNH: British Museum (Natural History), London, England
BOC: Bingham Oceanographic Collection, Peabody Museum, Yale University, New Haven, Conn.

CAS: California Academy of Sciences, San Francisco, Calif.
CBAT: Centro de Biologia Aquática Tropical, Lisboa, Portugal
CROA: Centres Recherches Océanographique, Abidjan, Côte d'Ivoire
CU: Cornell University, Ithaca, N.Y.
FMNH: Field Museum of Natural History, Chicago, Ill.
FSU: Florida State University, Tallahassee, Fla.
GCRL: Gulf Coast Research Laboratory, Ocean Springs, Miss.
HUJ: Hebrew University, Jerusalem, Israel
IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
ISFRS: Israel Sea Fisheries Research Station, Haifa, Israel
LACM: Los Angeles County Museum, Los Angeles, Calif.
MACN: Museo Argentina Ciencias Naturales, Buenos Aires, Argentina
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
MMF: Museu Municipal do Funchal, Madeira
MNHN: Muséum National d'Histoire Naturelle, Paris, France
MRAC: Musée Royal de l'Afrique Centrale, Tervuren, Belgium
SAM: South African Museum, Cape Town, South Africa
SIO: Scripps Institution of Oceanography, La Jolla, Calif.
SU: Stanford University, Division of Systematic Biology, Stanford, Calif.
TU: Tulane University, New Orleans, La.
UCLA: University of California, Los Angeles, Calif.
UF: University of Florida, Gainesville, Fla.
UMML: University of Miami Marine Laboratory, Miami, Fla.
UMMZ: University of Michigan Museum of Zoology, Ann Arbor, Mich.
UPR: University of Puerto Rico, Mayaguez, P.R.
USNM: U.S. National Museum, Washington, D.C.

Examination of these hosts yielded 488 collections of parasitic copepods containing 3,863 copepods (table 1). They represent 23 species (12 described for the first time herein) plus 8 more that were not described or assigned specific names because of the lack of sufficient material. All copepods are preserved in 70 percent ethyl alcohol and have been deposited in the USNM collections.

Type-specimens of the following copepod species were examined: *Caligus belones* Krøyer, *Lernanthropus belones* Krøyer, *Lernanthropus chlamydotes* Wilson, and *Caligodes megacephalus* Wilson.

In the formulas for spines and setae included in the descriptions, Roman numerals refer to spines and Arabic to setae.

The large numbers of copepods collected made it possible to evaluate statistically the variation of a particular character within each of three species: *Caligodes laciniatus*, *Parabomolochus bellones*, and *Lernanthropus tylosuri*. We compared host influence with geographical influence in these three species. We could have expanded such variational studies with our collections; however, this was not the primary purpose of the paper.

ACKNOWLEDGMENTS

We thank the curators of the many collections housing the needlefishes that we examined for copepods. Bruce Barrett picked copepods off many needlefishes while working as a volunteer in the summer of 1967. Robert Mathewson, Director of the Lerner Marine Laboratory, Bimini, Bahamas, and Jack Rudloe, Gulf Specimen Company, Panacea, Fla., sent us *Colobomatus*-infested specimens of *Strongylura notata* and *S. marina*. N. V. Parin, Institute of Oceanology, Moscow, sent us our first copepods from *Tylosurus choram*. Clyde S. Dawe, Laboratory of Pathology, National Cancer Institute, Bethesda, Md., provided us with a histopathological description of the *Colobomatus* swellings. Gerhard Gsell, also of the Laboratory of Pathology, prepared the photomicrographs (figs. 172–174). Mildred H. Carrington made the drawings of *S. notata* (fig. 170), *Caligodes* (fig. 146), and *Colobomatus* (fig. 171). Martin L. Wiley and Samuel Atsaides assisted with the statistical analyses. Thomas E. Bowman, Daniel M. Cohen, and Sneed B. Collard read the manuscript and made valuable suggestions.

TABLE 1.—*Summary of numbers of copepods found on each of the 28 species of needlefishes*

Needlefish species	Specimens examined	*Parabomolochus*				*Nothobomolochus*		*Caligodes laciniatus*	*Lernanthropus*		*Colobomatus goodingi*	*Lernealophus sultanus*	*Caligus* spp.	*Ergasilus*						*Acusicola*		*Paraergasilus remulus*	Species of copepods	Copepods
		bellones	*constrictus*	*eneiculus*	*sinensis*	*gibber*	*digitatus*		*tylosuri*	*belones*				*spatulus*	*argulus*	*coleus*	*semicoleus*	*orientalis*	*inflatipes*	*tenax*	*cunula*			
		Number																						
Ablennes hians	251	160	35	----	2	60	------	103	130	4	31	----	14	----	----	----	----	----	----	------	------	----	9	539
Belone belone	77	40	----	----	----	1	------	----	------	------	----	----	1	----	----	----	----	----	----	------	------	----	3	42
B. svetovidovi	15	1	----	----	----	4	------	----	------	------	----	----	----	----	----	----	----	----	----	------	------	----	2	5
Belonion apodion	15	----	----	----	----	------	------	----	------	------	----	----	----	----	----	----	----	----	----	------	------	----	0	0
B. dibranchodon	7	----	----	----	----	------	------	----	------	------	----	----	----	----	----	----	----	----	----	------	------	----	0	0
Lhotskia gavialoides	24	20	----	----	----	------	------	22	------	------	----	----	----	----	----	----	----	----	----	------	------	----	2	42
Petalichthys capensis	1	----	----	----	----	------	------	----	------	------	----	----	----	----	----	----	----	----	----	------	------	----	0	0
Platybelone argalus	487	48	65	----	----	157	------	1	1	2	----	----	72	----	----	----	----	----	----	------	------	----	7	346
Potamorrhaphis guianensis	63	----	----	----	----	------	------	----	------	------	----	----	----	----	----	----	----	9	----	------	------	----	1	9
Pseudotylosurus angusticeps	25	----	----	----	----	------	------	----	------	------	----	----	----	----	----	----	----	----	----	------	8	----	1	8
Strongylura anastomella	33	70	----	----	----	------	------	----	65	8	----	----	1	----	----	----	----	----	----	------	------	----	4	144
S. exilis	97	----	20	14	----	------	------	----	8	107	1	----	1	----	----	----	----	----	----	------	------	----	6	151
S. fluviatilis	33	----	----	----	----	------	------	----	------	------	----	----	----	----	58	----	----	----	----	------	------	----	1	58
S. incisa	75	6	----	----	----	------	------	----	1	16	----	----	3	----	----	----	----	19	----	------	------	----	5	45
S. krefftii	44	----	----	----	----	------	------	----	------	------	----	----	----	----	----	----	36	----	----	------	------	----	1	36
S. leiura	49	1	----	----	----	------	5	39	4	------	----	----	----	----	----	----	----	----	----	------	------	----	4	49
S. marina	316	119	----	----	----	------	------	----	5	172	6	1	----	23	----	----	----	----	----	203	------	----	7	529
S. notata	200	161	----	----	----	------	------	----	------	143	42	----	3	----	----	----	----	----	----	------	------	----	4	349
S. scapularis	38	----	15	139	----	------	------	----	------	12	----	----	----	----	48	----	----	----	----	------	------	----	4	214
S. senegalensis	27	5	----	----	----	------	------	----	------	------	----	----	----	----	----	----	----	----	62	------	------	----	2	67
S. strongylura	69	2	----	----	13	------	19	----	5	21	----	----	----	----	----	28	----	----	----	------	------	----	6	88
S. timucu	281	172	----	----	----	------	------	----	13	199	31	----	----	6	----	----	----	----	----	------	------	----	5	421
S. urvillii	21	1	----	----	----	------	------	----	1	------	----	----	1	----	----	4	----	----	----	------	------	----	4	7
Tylosurus acus	147	14	31	----	----	1	------	74	53	------	22	2	7	----	----	----	----	----	----	------	------	----	8	204
T. choram	18	----	----	----	----	------	------	7	1	------	----	----	1	----	----	----	----	----	----	------	------	----	3	9
T. crocodilus	212	25	12	----	----	12	1	128	185	------	57	----	17	----	----	----	----	----	----	------	------	----	8	437
T. punctulatus	31	----	----	----	----	------	3	----	2	5	----	----	----	----	----	----	----	----	----	------	------	----	3	10
Xenentodon cancila	65	----	----	----	----	------	------	----	------	------	----	----	----	----	----	51	----	----	----	------	------	3	2	54
Total number of specimens	2,721	845	178	153	15	235	28	374	474	689	190	3	121	29	106	83	36	28	62	203	8	3	XX	3,863
Total number of species	28	16	6	2	2	6	4	7	14	11	7	2	11	2	2	3	1	2	1	1	1	1	21+	XX

NEEDLEFISH COPEPODS

The accounts of the copepods found on needlefishes are arranged in three orders: Cyclopidea, Caligidea, and Philichthyidea.

Order Cyclopidea

Two families of cyclopid copepods were represented in the collections: Ergasilidae and Bomolochidae.

FAMILY ERGASILIDAE

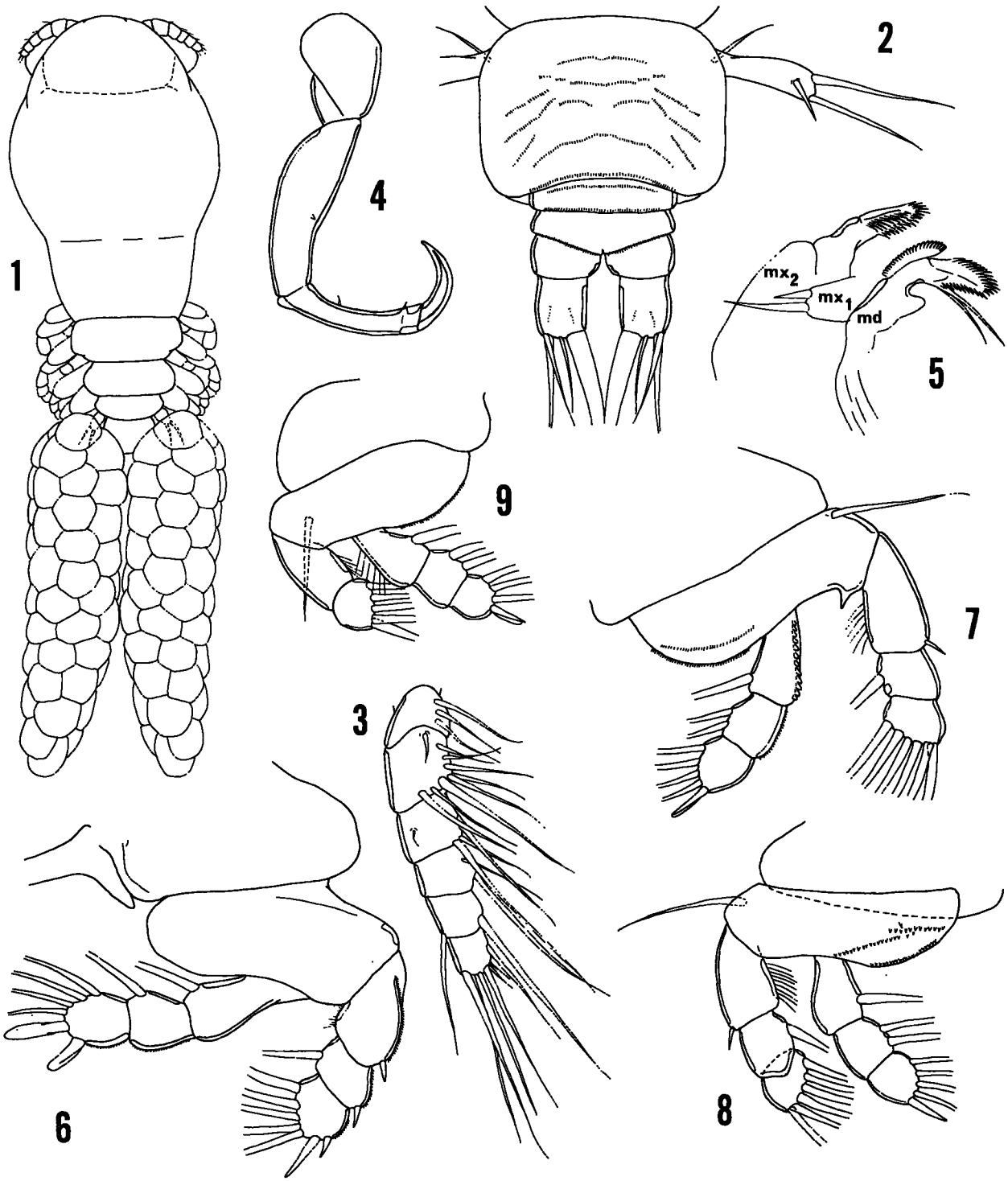
Eleven species of ergasilids were collected representing three genera; *Ergasilus*, *Paraergasilus*, and *Acusicola*, new genus. New species are described in each genus.

Ergasilus spatulus **Cressey, New Species**

Figures 1 to 9

Specimens studied.—Twenty-nine females from two collections from North America. The first collection containing the holotype female (USNM 125675) and 13 paratype females (USNM 125676) parasitic on the gill filaments of *Strongylura marina* (TU 6950) caught in Lake Pontchartrain, La. The second collection of six females is from the gill filaments of *S. timucu* and *S. marina* caught at Tortuguero, Costa Rica.

Female.—Body form as in figure 1. Total length 725 μ. Greatest width 363 μ measured at widest part of cephalon. First thoracic segment partially fused with head, composing cephalon. Cephalon 500 μ



FIGURES 1–9.—*Ergasilus spatulus*, new species, female. 1. Dorsal view. 2. Genital segment and abdomen including fifth leg, ventral view. 3. First antenna. 4. Second antenna. 5. Mouth parts (mandible, md; first maxilla, mx_1; second maxilla, mx_2). 6. First leg. 7. Second leg. 8. Third leg. 9. Fourth leg.

long, nearly 70 percent of total body length. Free thoracic segments, each succeeding one narrower than the one anterior to it. Genital segment (fig. 2) slightly wider than long (96 μ by 88 μ); rows of spinules on ventral surface as indicated in figure. Abdomen 3-segmented; each segment somewhat narrower than preceding one; terminal segment divided nearly entire length along medial anteroposterial line. Caudal rami nearly square (23 μ by 23 μ), with four terminal setae; innermost seta longest (190 μ) with base about half as wide as ramus.

First antenna (fig. 3) 6-segmented; all segments of nearly equal length, second slightly longer than others. Second antenna (fig. 4) in form of a claw; segments measure 89 μ, 221 μ, 118 μ, and 110 μ, respectively, devoid of ornamentation. Mouth parts (fig. 5) small and like other species of genus. Maxilliped absent.

Legs 1 to 4 biramose. Leg 1 (fig. 6) rami 3-segmented; two outer spines on endopod last segment spatulate. Leg 2 (fig. 7) rami 3-segmented; row of blunt spinules along outer edge of endopod first segment; spinelike process near inner edge of exopod on coxopod. Leg 3 (fig. 8) rami 3-segmented; coxopod with rows of spinules as indicated in figure. Leg 4 (fig. 9) exopod 2-segmented; endopod 3-segmented. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1.....	I:0	0:1	I:0	0:1	I:0	0:1	0:0	0:1
Seg. 2.....	I:1	0:1	0:1	0:2	0:1	0:2	5	0:2
Seg. 3.....	II:5	II:4	6	I:4	6	I:4	---	I:3

Leg 5 (fig. 2) a well-developed free segment bearing two terminal setae, one shorter subterminal seta, and one seta near base. Leg 6 absent.

Egg sacs long (640 μ), containing 50 to 60 eggs.

Color in life unknown.

Male.—Unknown.

Etymology.—The specific name *spatulus* is Latin for "a broad, flat tool" and refers to the nature of the endopod spines of leg 1.

Remarks.—This species may be separated from the other species of the genus by the row of spatulate spinules on the first endopod segment of leg 2 and by the broad spines on the last endopod segment of leg 1. This species appears to be very close to *Ergasilus arthrosis* Roberts.

Ergasilus argulus Cressey, New Species

Figures 10 to 16

Specimens studied.—Three collections containing 106 females from the Dagua River in Colombia, South America. The first collection containing the holotype female (USNM 125677) and 57 paratype females (USNM 125678) removed from the outer surface of the gill filaments of 5 *Strongylura fluviatilis* (CAS 11606). The other two collections from the gill filaments of *S. scapularis* caught in the mouth of the same river, 44 from 5 specimens (FMNH 59434–8) and 4 from 1 specimen (USNM 203520).

Female.—Body form as in figure 10. Total length 660 μ and greatest width 413 μ. Cephalon somewhat longer than wide (472 μ by 413 μ) with anterior portion subdivided. First thoracic segment fused with head. Width of free thoracic segments 218 μ, 160 μ, and 112 μ, respectively. Genital segment (fig. 11) 94 μ long and 106 μ wide with irregular row of spinules along posterior ventral border. Abdomen 3-segmented, each segment with row of spinules along posterior ventral border. Caudal rami nearly square, with four setae; longest seta 235 μ long; all setae sparsely plumose; short row of spinules on posterior ventral inner corner.

First antenna (fig. 12) 6-segmented; each segment with naked setae as in figure; segments measure 22 μ, 36 μ, 20 μ, 15 μ, 22 μ, and 18 μ in length, respectively. Second antenna (fig. 13) 4-segmented and in form of a claw; segments measure 195 μ, 384 μ, 295 μ, and 177 μ in length, respectively. Other mouth parts as in previous species. Maxillipeds absent.

Legs 1 to 4 biramose. Leg 1 (fig. 14) exopod 3-segmented; endopod 2-segmented; rami armed as in figure. Leg 2 (fig. 15) both rami 3-segmented, interpodal plate with row of prominent spinules along posterior border; both rami armed as in figure. Leg 3 same as leg 2. Leg 4 (fig. 16) exopod 2-segmented; endopod 3-segmented; rami armed as in figure; interpodal plate with spinules but less prominent than in legs 2 and 3. All setae on rami of legs 1 to 4 plumose. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1.....	1:0	0:1	1:0	0:1	1:0	0:1	0:0	0:1
Seg. 2.....	0:1	II:5	0:1	0:2	0:1	0:2	I:5	0:2
Seg. 3.....	II:5	-----	I:6	I:4	I:6	I:4	------	4

Leg 5 (fig. 11) a small knob bearing two naked setae. Leg 6 absent.

Egg sacs about 400 μ long, containing 28 to 32 eggs.

Color in life unknown; preserved material with purplish opaque spots scattered along middorsal line of body.

Male.—Unknown.

Etymology.—The specific name *argulus* refers to the resemblance of the cephalon to the branchiuran genus *Argulus*.

Remarks.—This species may be separated from other species of the genus with spinules on the intercoxal plates by a combination of the shape of the cephalon, shape of the egg sacs, and the rows of broad spinules on the genital and abdominal segments.

Ergasilus coleus Cressey, New Species

Figures 17 to 25

Specimens studied.—A single collection containing 4 females from *Strongylura urvillii* from the Philippines; three collections from *S. strongylura*, one with 4 females from Cagayan de Misamis, Mindanao, Philippines, one with 6 females from Sandakan Bay, Borneo, and one with 16 females from Porto Novo, Madras, India; two collections from *Xenentodon cancila*, one from USNM 149701 containing the holotype female (USNM 125679) and 10 paratype females (USNM 125680) from Travancore, India, and the other from SU 34948 with 40 females from Calcutta, India.

Female.—Body form as in figure 17. Total length 530 μ. Greatest width 210 μ. Cephalon subdivided; anterior portion bearing first and second antennae, posterior portion bearing mouth parts and first two thoracic legs. Thoracic segments bearing legs 3, 4, and 5 free. Genital segment (fig. 18) about twice as long as wide with thin wrinkled surface inconspicuously sclerotized. Abdomen 2-segmented; sclerotization heavier than in genital segment; articulation between segments obscure. Caudal rami small, nearly square, inner posterior corners produced to form stout spinelike processes; each ramus bearing three setae as indicated in figure.

First antenna (fig. 19) 6-segmented, armed as in figure. Second antenna (fig. 20) 4-segmented; first three segments enclosed in hyaline wrinkled sheath; claw of antenna free of sheath but piercing sheath of opposite second antenna as the two appendages encircle gill filament of host (sheath may provide soft surface for claw of opposite member to penetrate to secure copepod to host's gill). Mandible, first maxilla, and second maxilla (fig. 21) very small; mandible and second maxilla easily seen under oil immersion, but first maxilla reduced to a very small knob between these two and bearing a single short seta. Maxilliped absent.

Legs 1 to 4 biramose. Leg 1 (fig. 22) rami 3-segmented, outer distal spine on corner of exopod first segment very small. Leg 2 (fig. 23) rami 3-segmented; devoid of spines, setae arranged as in figure. Leg 3 (fig. 24) rami 3-segmented; devoid of spines as in leg 2, bearing one additional seta on exopod last segment; outer seta on endopod last segment short. Leg 4 (fig. 25) exopod 2-segmented; endopod 3-segmented; rami armed as in figure. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	0:0	0:1	0:0	0:1	0:0	0:1
Seg. 2	0:1	0:1	0:1	0:1	0:1	0:1	5	0:2
Seg. 3	II:5	II:3	4	5	5	4	.....	4

Leg 5 (see fig. 18) a free segment with two terminal setae and one seta near base (a subterminal seta could not be found). Segment bearing leg 5 fused with genital segment. Leg 6 absent.

Egg sac 480 μ long, bearing about 40 eggs.

Color in life unknown.

Male.—Unknown.

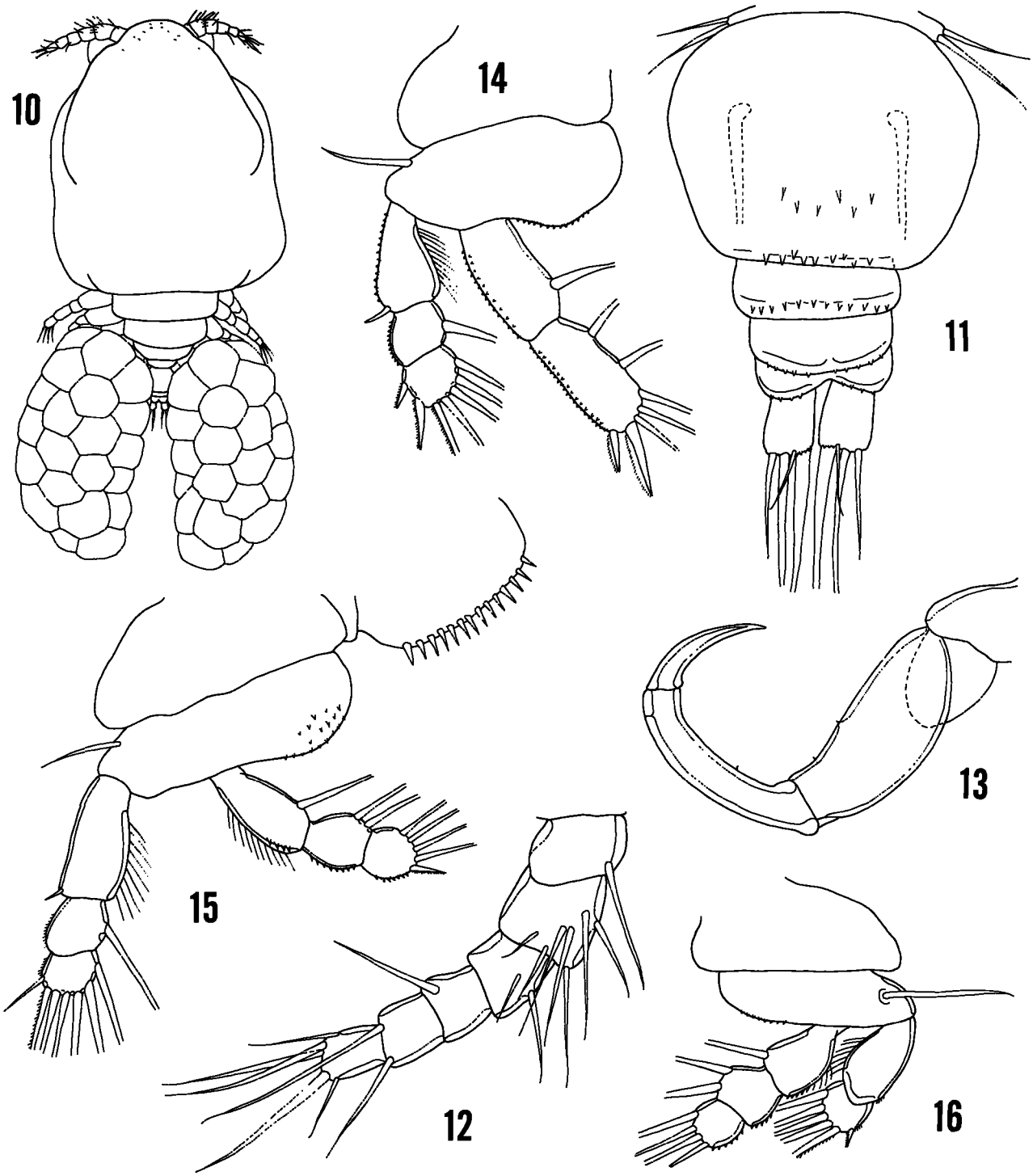
Etymology.—The specific name *coleus* is Latin for "sheath" and refers to the nature of the second antenna.

Remarks.—This species may be separated from all known species of *Ergasilus*, except *E. amplectens* Dogiel and Akhterov (1952) by the presence of the sheath surrounding the second antenna. It differs from *amplectens* by the nature of the genital segment; in *amplectens* the genital segment and abdomen are well defined, whereas in *coleus* the genital segment appears to be encased in a sheath similar to that on the second antenna.

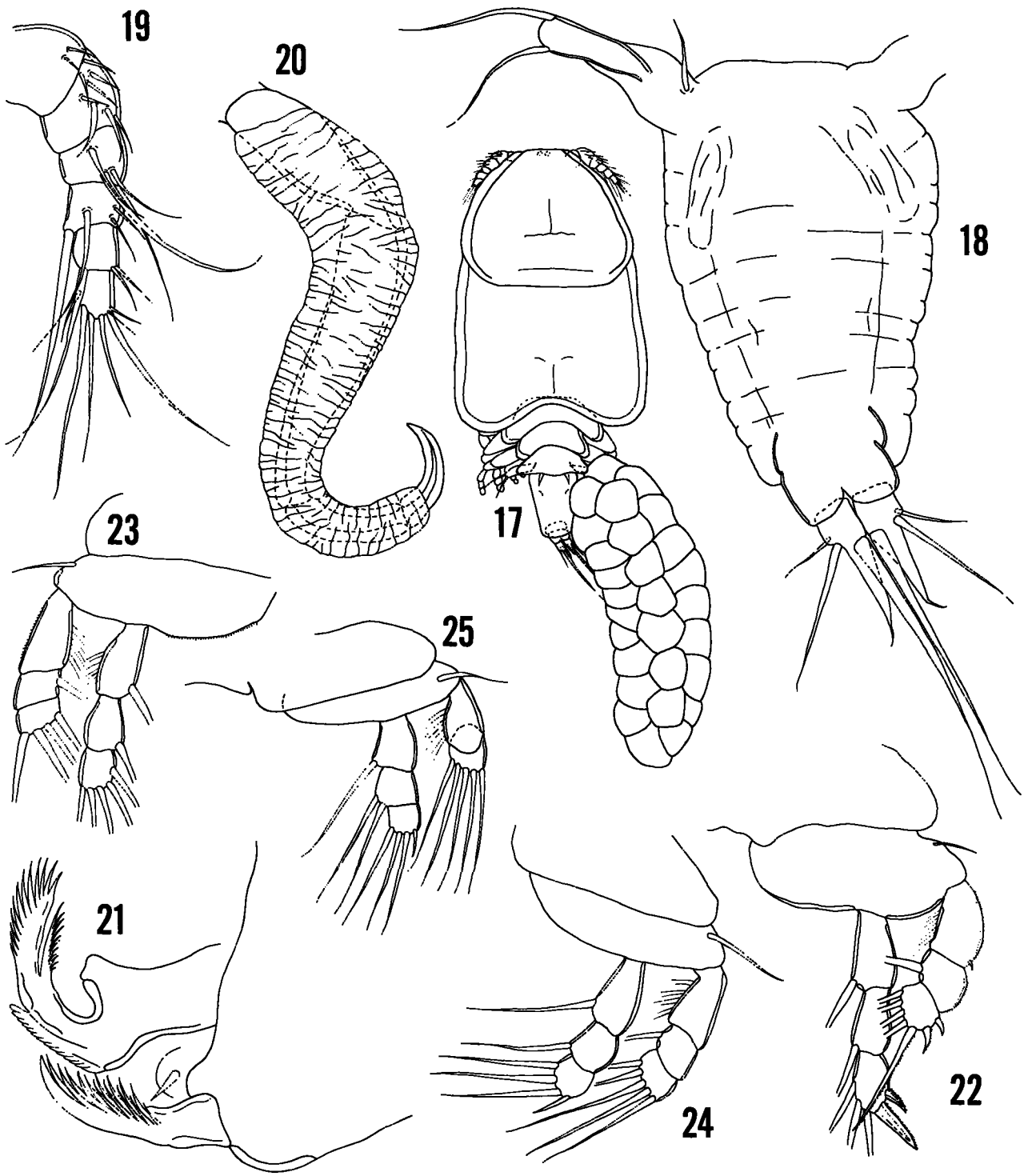
Ergasilus semicoleus Cressey, New Species

Figures 26 to 32

Specimens studied.—A single collection from the gill filaments (mostly in upper branchial area—between demibranchs of 4th gill arch) of six *Strongylura krefftii* (USNM 173999) from a large



FIGURES 10–16.—*Ergasilus argulus*, new species, female. 10. Dorsal view. 11. Genital segment and abdomen, including fifth leg, ventral view. 12. First antenna. 13. Second antenna. 14. First leg. 15. Second leg. 16. Fourth leg.



FIGURES 17–25.—*Ergasilus coleus*, new species, female. 17. Dorsal view. 18. Genital segment and abdomen, including fifth leg, ventral view. 19. First antenna. 20. Second antenna. 21. Mouth parts. 22. First leg. 23. Second leg. 24. Third leg. 25. Fourth leg.

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billabong at Oenpalli on the Alligator River, Arnhem Land, Australia. Holotype female (USNM 125681) and 35 paratype females (USNM 125682).

Female.—Body form as in figure 26. Total length 725 μ. Greatest width 295 μ measured at widest part of posterior portion of cephalon. Cephalon subdivided as in *E. coleus*, but posterior lobe bearing mouth parts and first thoracic legs only. Thoracic segments bearing legs 2, 3, 4, and 5 free. Genital segment (fig. 27) as wide as long (81 μ by 81 μ). Abdomen 3-segmented, each segment somewhat narrower than preceding. Caudal rami short, inner distal corner produced to form stout spine-like process; each ramus with three additional setae.

First antenna (fig. 28) 6-segmented and armed as in figure. Second antenna (fig. 29) 4-segmented; second segment enveloped in a thin sheath, surface of sheath somewhat wrinkled in appearance (not as much as in *E. coleus*). Second antennae completely encircle a gill filament of host. Mouth parts as in previous species. Maxillipeds absent.

Legs 1 to 4 biramose. Leg 1 (fig. 30) rami 3-segmented, armed as in figure. Leg 2 (fig. 31) rami 3-segmented, armed as in figure. Leg 3 similar to leg 2 except last exopod segment with six setae and last endopod segment with four setae and one spine. Leg 4 (fig. 32) exopod 2-segmented; endopod 3-segmented, armed as in figure. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1.....	I:0	0:0	I:0	0:0	I:0	0:0	I:0	0:1
Seg. 2.....	0:1	0:1	0:1	0:1	0:1	0:1	5	0:2
Seg. 3.....	II:6	II:5	5	I:3	I:4	6	.....	I:3

Leg 5 (see fig. 27) a free segment bearing two terminal setae—one subterminal and one near base of free segment. Leg 6 absent.

Egg sacs 500 μ long and containing 25 to 30 eggs.

Color in life unknown.

Male.—Unknown.

Etymology.—The specific name *semicoleus* is Latin for "half sheath" and refers to the nature of the second antenna.

Remarks.—This species differs from all other known species in having half of the second antenna encased in a sheath. It seems to be closely related to *E. coleus* and *E. amplectens* based on the presence of this sheath and other characters common to all three species.

Ergasilus inflatipes Cressey, New Species

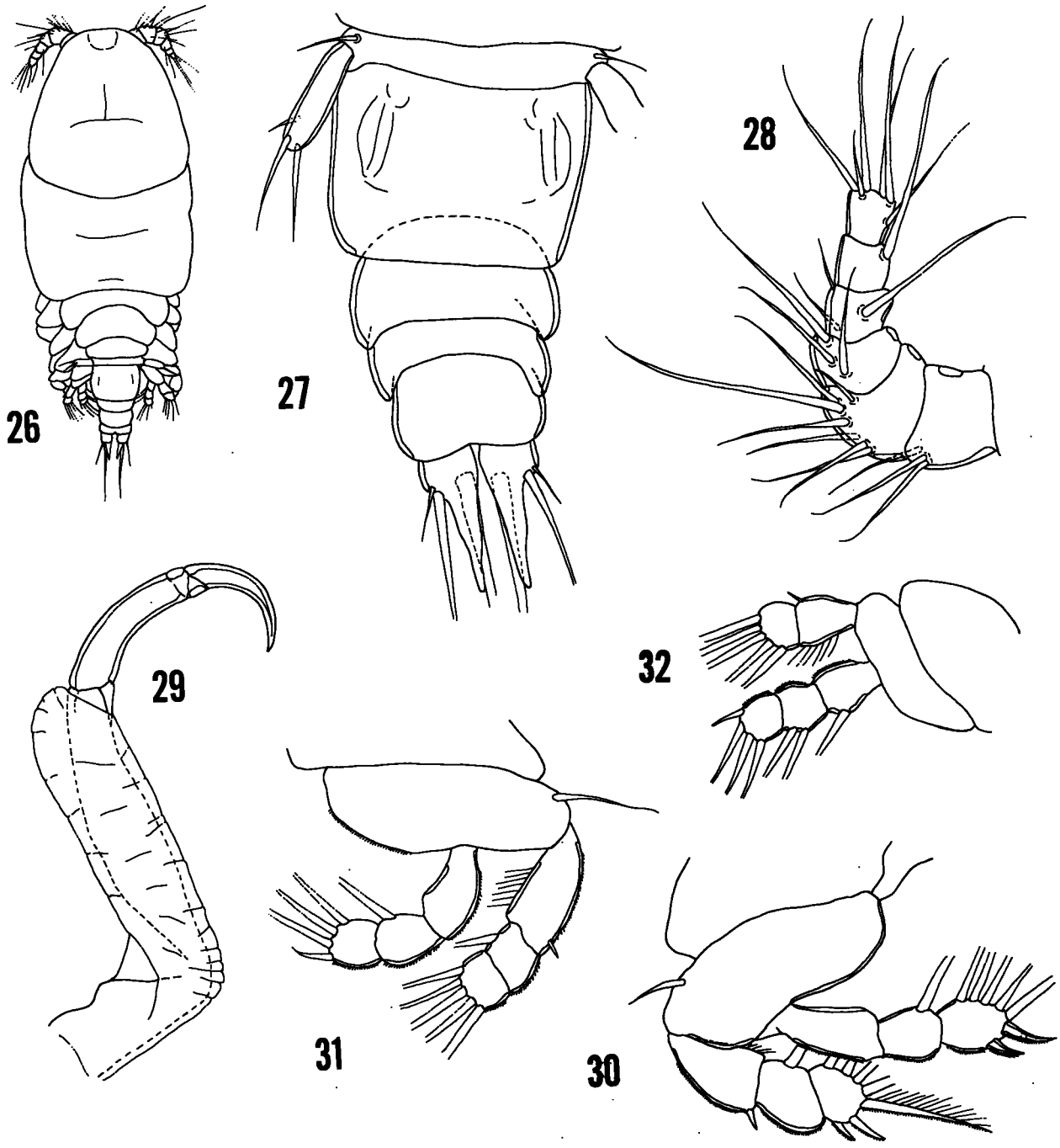
Figures 33 to 41

Specimens studied.—Three collections containing 28 females from *Strongylura senegalensis* from the Volta River, Ghana, and a single collection with 33 females from the same host from Ebzie Lagoon, Ivory Coast. Holotype female (USNM 125683) and 8 paratype females (USNM 125684) from one of the Ghana specimens.

Female.—Body form as in figure 33. Total length 625 μ. Greatest width 354 μ measured at widest part of cephalon. Cephalon not subdivided dorsally as in previous two species. Thoracic segments bearing legs 1 to 5 free, each one narrower than preceding segment. Genital segment (fig. 34) slightly wider than long (88 μ by 74 μ). Abdomen (fig. 34) 3-segmented; anterior two segments each with two interrupted transverse rows of spinules and last abdominal segment with a row of fine spinules along posterior border, all on ventral surface. Caudal rami short, about as wide as long and bearing four setae, innermost considerably longer and wider at base than other three.

First antenna (fig. 35) 6-segmented; first two segments incompletely divided, each segment armed as in figure with a plumose seta present on each of the last three segments. Second antenna (fig. 36) in shape of claw with no distinguishing characters. Mouth parts as in figure 37; mandible with single seta near base of terminal process; first maxilla a small lobe with three setae; second maxilla with single seta on terminal segment near base of spinose tip. Maxillipeds absent.

Legs 1 to 4 biramose. Leg 1 (fig. 38) rami 3-segmented, armed as in figure. Leg 2 (fig. 39) rami 3-segmented; coxopod with rows of fine spinules; rami with spines and setae as in figure. Leg 3 identical to leg 2. Leg 4 (fig. 40) exopod 2-segmented; endopod 3-segmented; rami armed as in figure. Leg 5 (fig. 41) with free segment bearing three setae, outer two plumose; single seta near base of free segment. Leg 6 absent.



FIGURES 26–32.—*Ergasilus semicoleus*, new species, female. 26. Dorsal view. 27. Genital segment and abdomen, including fifth leg, ventral view. 28. First antenna. 29. Second antenna. 30. First leg. 31. Second leg. 32. Fourth leg.

Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1.....	I:0	0:1	1:0	0:1	1:0	0:1	1:0	0:0
Seg. 2.....	I:1	0:1	0:1	0:2	0:1	0:2	5	0:2
Seg. 3.....	II:5	II:4	6	I:4	6	I:4	---	I:2

Egg sacs long (650μ), containing about 40 eggs. Color in life unknown.

Male.—Unknown.

Etymology.—The specific name *inflatipes* is Latin for "swollen foot" and refers to the shape of the fifth leg.

Remarks.—This species can be separated from all described species of the genus by the nature of the fifth leg. Yamaguti (1963, p. 28) stated that the first maxilla of *Ergasilus* has two setae; this species has three. It does not seem justifiable to erect a new genus on the basis of this character difference alone but *E. inflatipes* can apparently be further separated from all other species in the genus by this difference.

***Ergasilus orientalis* Yamaguti**

Figure 42

Yamaguti (1939a, p. 393) described *Ergasilus orientalis* from *Acanthogobius flavimanus* (Gobiidae) and *Atherina bleekeri* (Atherinidae) from Japan. A single collection of 19 females of this species from 1 specimen of *Strongylura incisa* (USNM 174005) caught near the mouth of the Emerald River, Groote Eylandt, Arnhem Land, Australia, is reported here, plus a single collection of 9 females from *Potamorrhaphis guianensis* (MCZ 8788) from Gurupá, Brazil, near the mouth of the Amazon River.

Female.—The description provided by Yamaguti is adequate, and, except for a figure of an Australian female (fig. 42) and its measurements, no further description is given here.

Total length 790 μ. Greatest width 325 μ. Cephalon 590 μ long, 325 μ wide. Anterior portion of cephalon separate lobe measuring 230 μ by 230 μ. Egg sacs 725 μ long, containing 50 to 60 eggs.

Remarks.—No differences could be found between the two populations referred to *E. orientalis*. The South American population may represent a separate, apparently identical species.

***Ergasilus* Sp. A**

A single female was collected from the gill filaments of *Strongylura marina* (USNM 114589) from Lake Yzabel, Guatemala; two additional females were collected from the gill filaments of *S. timucu* (USNM 114314) from 20 miles above the mouth of the Río Sarston on the Guatemala-British Honduras border. This copepod appears to be the same as the specimen described and figured by Thomsen (1949) as *E. lizae* from *Mugil braziliensis* from the Río de la Plata near Montevideo, Uruguay. Thomsen's material plus the three specimens reported here probably represents an undescribed species, but it seems best not to name it until more material is available and a complete description can be provided.

***Ergasilus* Sp. B**

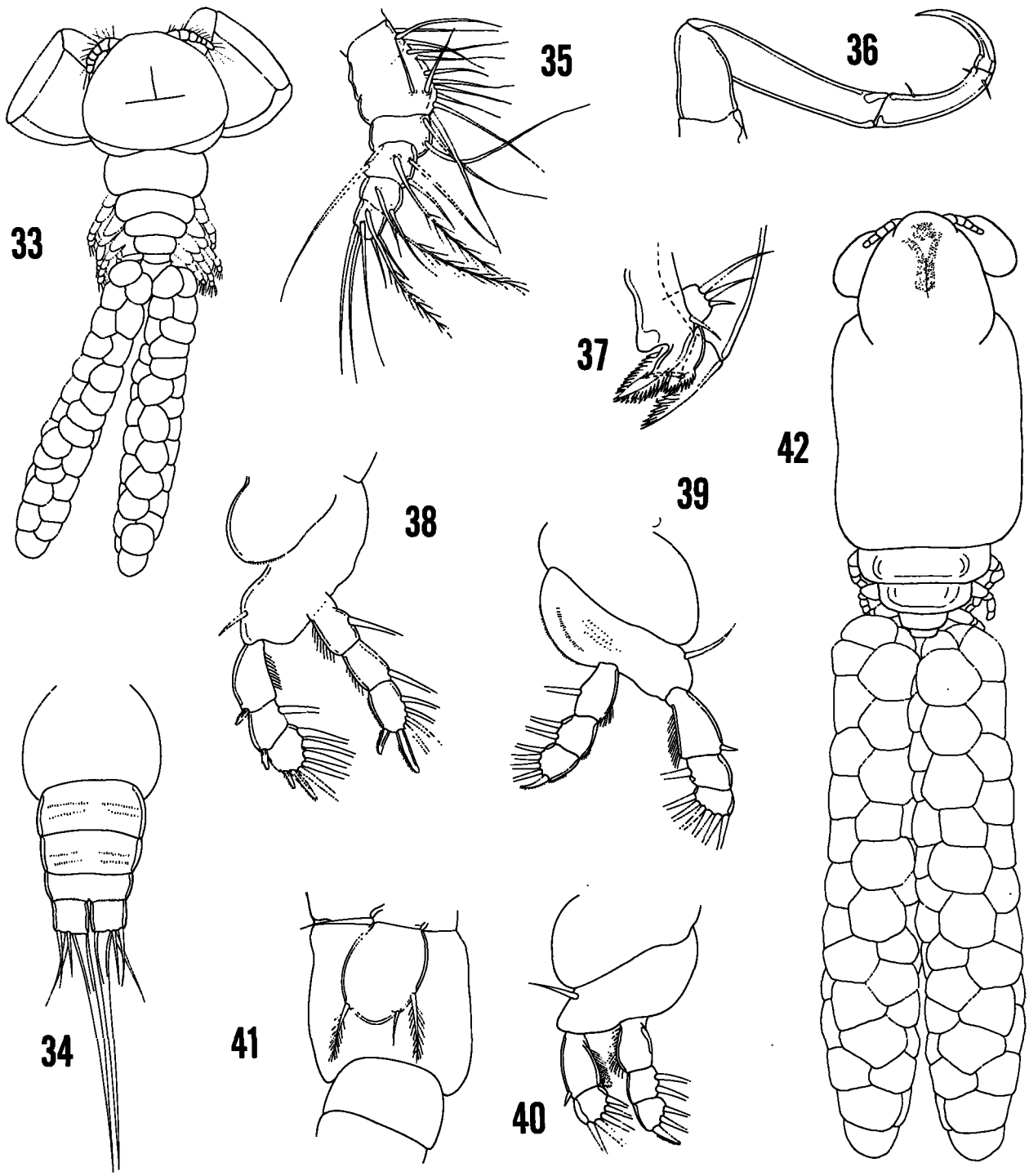
One female from the gill filaments of *Xenentodon cancila* (FMNH 58917) collected in Ceylon. It has not been described as a new species because only one specimen was available. The following characters were noted, however, and are presented to aid future workers.

This species is closely related to *Ergasilus coleus* and *E. semicoleus* described above. The second antenna is sheathed nearly its entire length, but the sheath is not as conspicuous as in *E. coleus*. The degree of segmentation of the abdomen is intermediate between the lack of segmentation in *E. coleus* and the well-defined segments of *E. semicoleus*. In the species discussed here, the three abdominal segments are separate; each of the posterior two segments has a single transverse row of spinules on its ventral surface. The genital segment bears two transverse rows of spinules on its ventral surface. The caudal rami are similar to those of *E. coleus* and *E. semicoleus*.

Ergasilus coleus also was collected from *Xenentodon* in India.

***Acusicola* Cressey, New Genus**

Ergasilidae. Male unknown. Female: Thoracic segments bearing legs 1 to 4 free. Abdomen 3-segmented. First antenna 5-segmented. Second antenna 5-segmented; terminal three segments very short, combined length of all three about one-half length of second segment. Maxilliped absent. Legs 1 to 4 biramose; leg 1 endopod 2-segmented; leg 4 exopod 2-segmented; all other rami 3-segmented. Leg 5 a short papilla at the distal outer



FIGURES 33–42.—*Ergasilus* species. 33–41. *E. inflatipes*, new species, female. 33. Dorsal view. 34. Genital segment and abdomen, ventral view. 35. First antenna. 36. Second antenna. 37. Mouth parts. 38. First leg. 39. Second leg. 40. Fourth leg. 41. Fifth leg, lateral view. 42. *E. orientalis* Yamaguti, female, dorsal view.

border of genital segment bearing a single seta. Leg 6 absent.

Acusicola differs from all other known genera of ergasilids except *Paraergasilus*, *Ergasiloides*, and *Thersitina* by having a 5-segmented first antenna. It differs from *Ergasiloides* by having a 3-segmented abdomen (*Ergasiloides* has only one segment), from *Thersitina* by the presence of maxillipeds in *Thersitina*, and from *Paraergasilus* by the nature of the second antenna.

The generic name is Latin, *acus* for "needle" and *cola* for "inhabitant" and refers to the fact that the first two species of the genus are reported from needlefishes.

Type-species.—*Acusicola tenax*.

Acusicola tenax (Roberts)

Figures 43 to 52

Specimens studied.—A single collection containing 203 females removed from the outer tips of the gill filaments (usually the upper filaments) of 17 *Strongylura marina* (UMMZ 143506) caught at Río de la Pasíon, Peten, Guatemala. An additional collection of two females from one *S. marina* caught at El Quiche, Guatemala.

Female.—Body form as in figure 43. Total length 800 μ; greatest width 225 μ. Thoracic segments bearing legs 1 to 4 separated from head. Thoracic segments decreasing in width from first to fourth. Genital segment about as wide as long (100 μ by 100 μ). Abdomen (fig. 44) 3-segmented; second and third segments only slightly narrower than preceding one. Caudal rami about twice as long as wide (44 μ by 21 μ), with three long terminal setae (longest about 175 μ long) and one short median one; patch of spiniforms on ventral surface near distal end of each ramus.

First antenna (fig. 45) 5-segmented; first segment longest (60 μ) with remaining four each about half as long, armed as in figure. Second antenna (fig. 46) 5-segmented; segments measure 103 μ, 325 μ, 60 μ, 60 μ, and 30 μ, respectively, and unarmed. Mandible (fig. 47) armed as in figure. First maxilla a small knob with two setae between mandible and second maxilla. Second maxilla (fig. 48) with brushlike tip.

Legs 1 to 4 biramose. Leg 1 (fig. 49) exopod 3-segmented, each segment with spinulose outer margins; endopod 2-segmented, each segment with spinulose outer margins and strong clawlike spine on end of terminal segment. Leg 2 (fig. 50) both rami 3-segmented; one spine on outer distal corner of exopod first segment, otherwise armed with setae as in figure. Leg 3 (fig. 51) both rami 3-segmented; spine on outer distal corner of exopod first segment plus weak spine at terminus of endopod, otherwise armed with setae as in figure. Leg 4 (fig. 52) exopod 2-segmented, outermost terminal seta unusually long and conspicuous; endopod 3-segmented with weak spine on outer corner of terminal segment, otherwise armed with setae as in figure.

Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	I:0	0:1	I:0	0:1	0:0	0:0
Seg. 2	0:1	I:4	0:1	0:2	0:1	0:2	4	0:2
Seg. 3	I:6	---	6	5	6	5	---	I:3

Leg 5 a small papilla bearing one seta near anterior outer corners of genital segment. Leg 6 absent.

Egg sac about 500 μ long, bearing 28 to 32 eggs.

Color in life unknown.

Male.—Unknown.

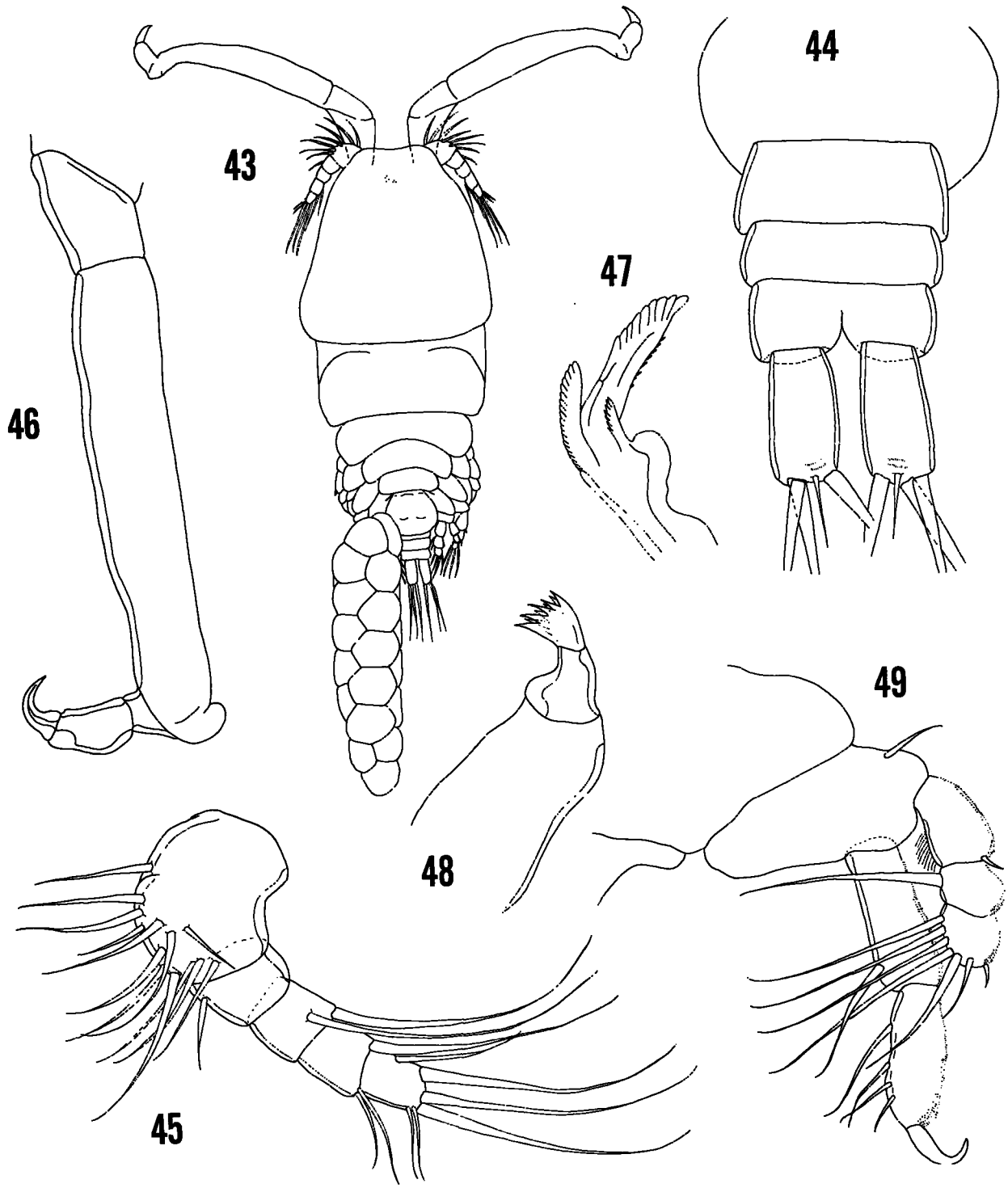
Remarks.—The copepods came from a freshwater population of *Strongylura* now referred to *S. marina* but possibly representing an undescribed form. *Acusicola tenax* was previously reported by Roberts (1965) from Texas as a parasite of *Pomoxis annularis*.

Acusicola cunula Cressey, New Species

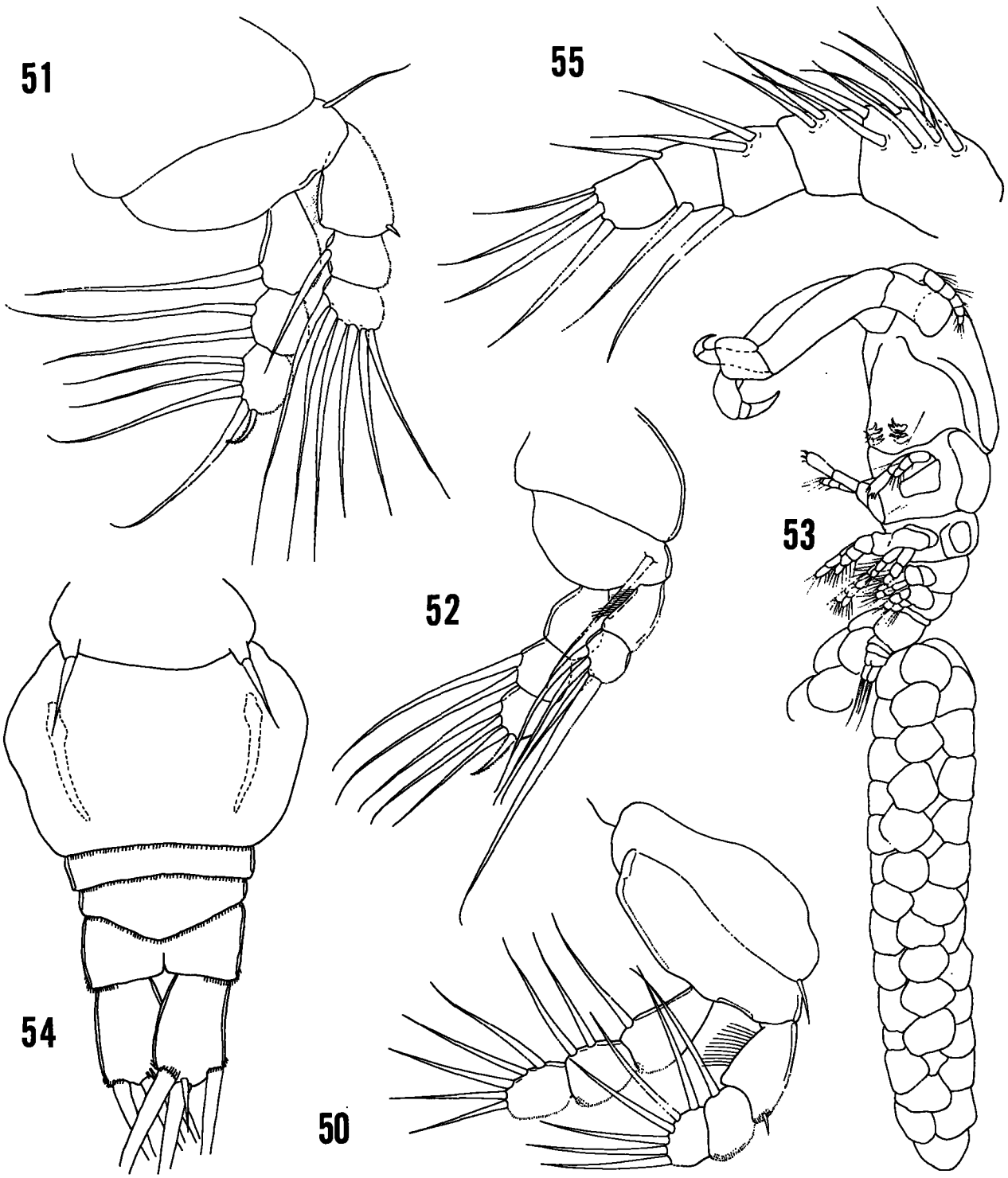
Figures 53 to 60

Specimens studied.—Eight females from two collections from the gill filaments of *Pseudotylosurus angusticeps* collected from Brazil. Holotype female (USNM 125687), two paratype females (USNM 125688) from a single host fish (MCZ 8797) collected at Porto do Moz, near the mouth of the Amazon River, Brazil. Exact locality data for second collection in Brazil (host fish—MCZ 8790) unknown, second collection contains six females.

Female.—Body form as in figure 53. Total length 652 μ. Greatest width 290 μ. Thoracic segments bearing legs 1 to 4 free. Genital segment (fig. 54) slightly wider than long. Abdomen 3-segmented; ventral posterior border with row of spinules on each segment, last segment row confined to outer corners. Caudal rami longer than wide (38 μ by 24 μ); rows of spinules on ventral



FIGURES 43–49.—*Acusicola tenax* female. 43. Dorsal view. 44. Genital segment and abdomen, ventral view. 45. First antenna. 46. Second antenna. 47. Mandible. 48. Second maxilla. 49. First leg.



FIGURES 50–55.—*Acusicola*, new genus. 50–52. *A. tenax* female (continued). 50. Second leg. 51. Third leg. 52. Fourth leg. 53–55. *A. cunula*, new species, female. 53. Lateral view. 54. Genital segment and abdomen, ventral view. 55. First antenna.

distal corners, otherwise armed as in previous species.

First antenna (fig. 55) 5-segmented; basal segment largest, remaining four all of about same length, armed as in figure. Second antenna (fig. 56) 5-segmented; second segment longer than other four combined, third segment with shieldlike process originating at base and surrounding entire inner surface of segment plus part of fourth segment, claw of antenna cradled in this shieldlike process. Mandible, first and second maxilla (fig. 57) similar to preceding species; maxilla larger than in *A. tenax*, with two setae. Maxilliped lacking.

Legs 1 to 4 biramose. Leg 1 (fig. 58) exopod 3-segmented, spine on outer distal corner of first segment and two spines on outer edge of last segment, otherwise armed with setae as in figure; endopod 2-segmented, two short spines on terminus of ramus, outer edge of both segments with numerous spinules, setae arranged as in figure. Leg 2 (fig. 59) rami 3-segmented; one spine on outer distal corner of exopod last segment, otherwise rami armed with setae as in figure. Leg 3 as leg 2. Leg 4 (fig. 60) exopod 2-segmented; endopod 3-segmented, with a spine on outer distal corner of terminal segment, otherwise rami with setae as in figure. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	0:0	0:1	0:0	0:1	0:0	0:1
Seg. 2	0:1	II:4	0:1	0:2	0:1	0:2	5	0:2
Seg. 3	II:5	----	I:6	5	I:6	5	----	I:3

Leg 5 (fig. 54) papilla with one seta near anterior corner of genital segment. Leg 6 absent.

Egg sac 945 μ long, containing about 50 eggs.

Color in life unknown.

Male.—Unknown.

Etymology.—The specific name *cunula* is Latin for "small cradle" referring to the cradlelike structure on the second antenna.

Remarks.—This species may be distinguished from *A. tenax* by the nature of the second antenna and the first leg. These two species may be further separated by the differences in the spine and seta formulas for legs 1 to 4.

Paraergasilus remulus Cressey, New Species

Figures 61 to 70

Specimens studied.—A single collection from *Xenentodon cancila* (UMMZ 181174) collected in a tributary of Prek Andhor, Cambodia. Holotype female (USNM 125689) and one paratype female (USNM 125690) attached to upper inner surface of operculum (not on gill filaments) of host.

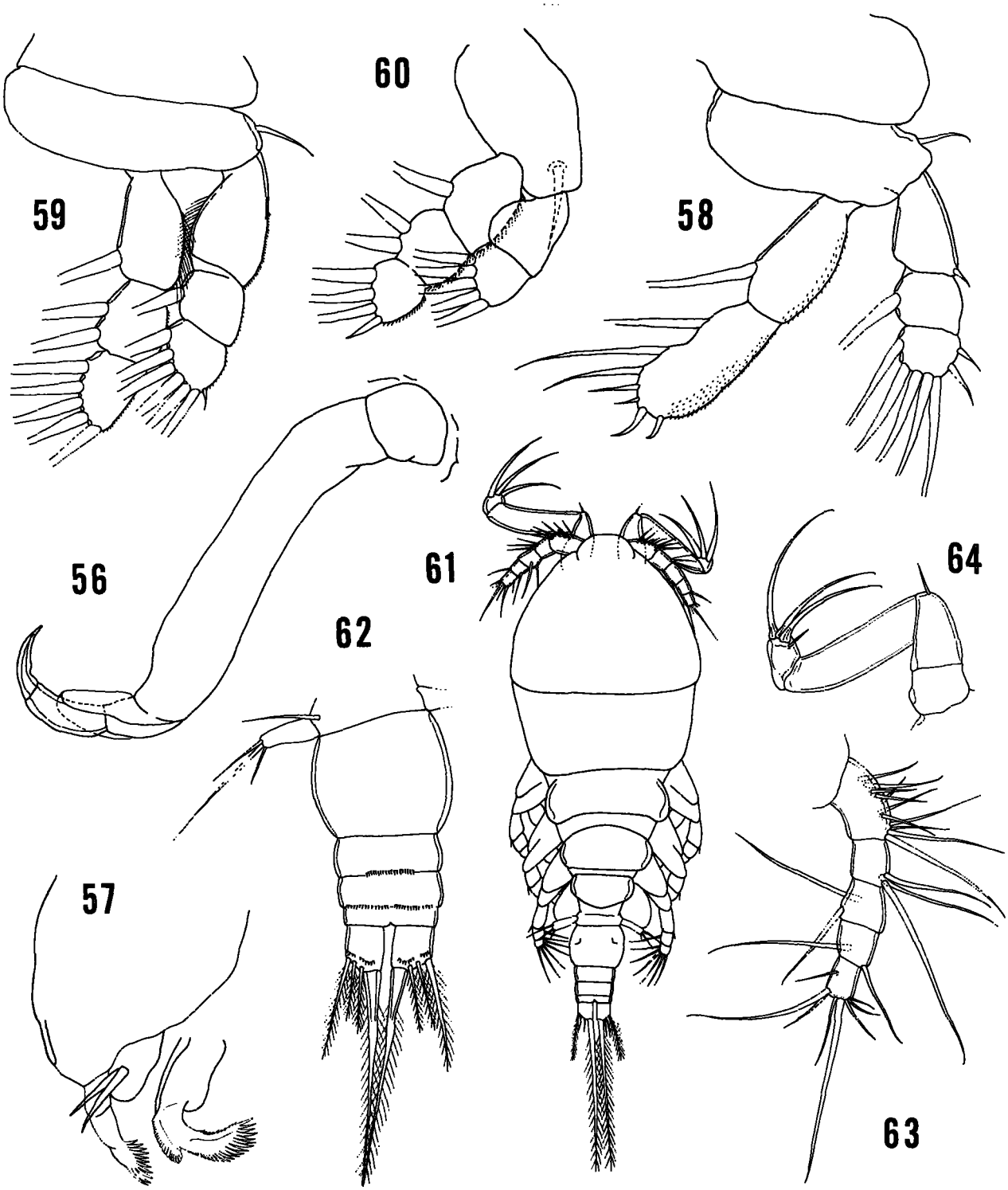
Female.—Body form as in figure 61. Total length 443 μ. Greatest width 153 μ. Thoracic segments bearing legs 2 to 4 free. Thoracic segment bearing leg 1 separated from cephalon, articulation weak giving appearance of segment being incorporated into cephalon. Thoracic segments bearing legs 2 to 4, each narrower than preceding segment. Genital segment (fig. 62) slightly wider than long (47.8 μ by 41.3 μ). Abdomen (fig. 62) 3-segmented, first two each with a row of spinules along the ventral posterior border as in figure. Caudal rami slightly longer than wide (16.5 μ by 14.7 μ), with four terminal setae, innermost considerably longer (90 μ) than other three and with a bulbous swelling about 20 μ from base; ventral surface of ramus with an interrupted row of spinules near base of setae.

First antenna (fig. 63) 5-segmented and armed with numerous delicate setae. Second antenna (fig. 64) 4-segmented; second segment with a short seta on outer distal corner; terminal segment with three long terminal setae and one short subterminal seta. Mandible (fig. 65), first maxilla (fig. 66), and second maxilla (fig. 67) very small; even at a magnification of 1,500x, it was difficult to make out details of these three appendages. Maxilliped absent.

Legs 1 to 4 biramose. Rami of legs 1, 2, and 3, 3-segmented. Leg 1 (fig. 68) coxopod with row of spinules; last segment of endopod bearing two broad spines in addition to four setae. Leg 2 (fig. 69) and leg 3 the same in appearance. Leg 4 (fig. 70) exopod 2-segmented, endopod 3-segmented; each armed as in figure. All setae on legs 1 to 4 plumose. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	I:0	0:1	I:0	0:1	I:0	0:1
Seg. 2	0:1	0:1	0:1	0:0	0:1	0:0	I:5	0:1
Seg. 3	II:4	II:4	6	I:4	6	I:4	---	I:3

373-320 O—70——3



FIGURES 56–64.—*Acusicola*, new genus, and *Paraergasilus*. 59–60. *A. cunula*, new species, female (continued). 56. Second antenna. 57. Mouth parts. 58. First leg. 59. Second leg. 60. Fourth leg. 61–64. *P. remulus*, new species, female. 61. Dorsal view. 62. Genital segment and abdomen, ventral view. 63. First antenna. 64. Second antenna.

Leg 5 (see fig. 62) a free segment with three setae at its tip and an additional seta near its base on thoracic segment. Leg 6 absent.

No egg sacs present on material studied.

Male.—Unknown.

Etymology.—The specific name *remulus* is Latin for "oar" and refers to the nature of the broad spatulate spines on the tip of the endopod of leg 1.

Remarks.—This species may be distinguished from the six known species of *Paraergasilus* by the two broad spines on the tip of the endopod of leg 1. Fryer (1968) stated that *Paraergasilus* is probably restricted to the nasal sinuses of the hosts. The two specimens reported here were found attached beneath the operculum. The nasal fossae of all synentognath fishes are open pits so it would be difficult for any copepod to attach therein. In any event, it seems apparent that members of this genus are not found on the gills as Yamaguti (1963) has reported.

All known species of *Paraergasilus* have been collected from Asia or East Africa.

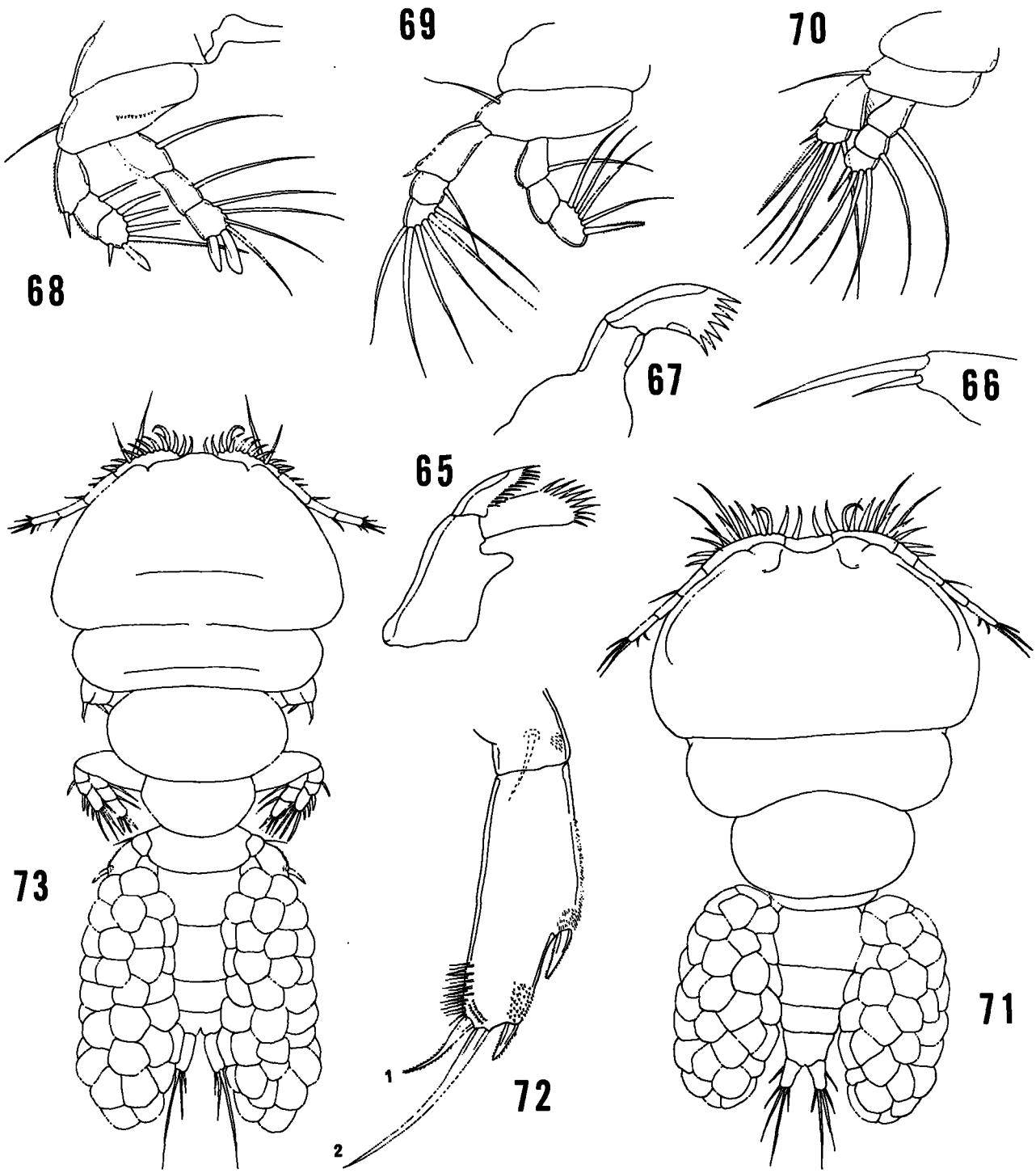
FAMILY BOMOLOCHIDAE

Six species of bomolochids were collected representing the genera *Parabomolochus* and *Nothobomolochus*. Four of the six species discussed are new.

Parabomolochus bellones (Burmeister)

Figures 71, 72

Specimens studied.—A total of 860 individuals from the gill chambers and oral valves of 16 species of hosts: *Ablennes hians* (gill chambers), Woods Hole, Mass.; Virginia coast (3 collections); north Florida; Florida Keys; Gulf of Mexico, lat. 28°30′ N., long. 88°45′ W. (2 collections); Haiti; British Honduras (3 collections); Padre Bank, Caribbean Sea; Grand Bahama Island; off North Brazil (2 collections); Gulf of Guinea (7 collections); Liberia; Persian Gulf; Natal, South Africa; Red Sea; Japan (4 collections); *Belone belone* (gill chambers), "Europe" (2 collections); Trieste; Venice, Italy (2 collections); Naples, Italy; Mediterranean Sea; Tunisia; Spain (2 collections); *Belone svetovidovi* (gill chambers), Genoa, Italy; *Platybelone argalus* (gill chambers), Puerto Rico (2 collections); Cuba; Gulf of Mexico, lat. 20°12′ N., long. 91°59′ W., Cay Arcas, Gulf of Mexico; Cumana, Venezuela; Saudi Arabia; *Strongylura anastomella* (gill chambers), Matsushima, Japan; "Japan" (5 collections); Yokohama, Japan (2 collections); Suruga Bay, Japan; Sea of Japan; Chiba Prefecture, Japan; Korea; *Strongylura leiura* (gill chambers), Hong Kong; *Strongylura incisa* (gill chambers), Philippine Islands (2 collections); *Strongylura marina* (gill chambers and oral valves), Martha's Vineyard, Mass.; Morehead City, N.C.; Beaufort, N.C. (4 collections); Southport, N.C.; St. Simons Island, Ga. (4 collections); Jekyll Island, Ga.; Amelia River, Fla.; Flagler Beach, Fla.; Key West, Fla.; Everglades Park, Fla.; Sanibel Island, Fla.; Alligator Harbor, Fla. (3 collections); Yucatan, Mexico; Panama (Atlantic); Cumana, Venezuela; Venezuela; Trinidad; *Strongylura notata* (gill chambers and oral valves), Sarasota, Fla. (4 collections); New Smyrna, Fla.; Banana River, Fla.; Key Biscayne, Fla. (7 collections); Matecumbe Key, Fla.; Bayport, Fla.; Alligator Harbor, Fla.; Pensacola, Fla.; Andros Island, Bahamas; Mujeres Island, Yucatan; Tampico, Mexico; Havana, Cuba (2 collections); Palisadoes, Jamaica; *Strongylura senegalensis* (gill chambers and oral valves), Ivory Coast (2 collections); Volta River, Ghana; *Strongylura strongylura* (gill chambers), Arnhem Land, Australia; *Strongylura timucu* (gill chambers), Sarasota, Fla.; Pensacola, Fla.; Placida, Fla.; Clearwater, Fla.; Monroe County, Fla.; Tampa Bay, Fla.; Key Biscayne, Fla. (2 collections); Sanibel Island, Fla.; Virgin Gorda Sound, Virgin Islands; Mayaguez, Puerto Rico; Laguna Rincon, Puerto Rico; Cabo Rojo, Puerto Rico; San Juan, Puerto Rico; Punta Arenas, Puerto Rico; Port-au-Prince, Haiti; Lazaretto, Jamaica; St. Thomas, Virgin Islands; New Providence, Bahamas; Ascension Bay, Yucatan; Progresso, Yucatan; Honduras; *Strongylura urvillii* (gill chambers), Philippine Islands; *Tylosurus acus* (gill chambers and oral valves), Gulf of Mexico, lat. 20°50′ N., long. 93°00′ W.; off North East Florida; Monroe County, Fla.; Honduras; Freetown, Sierra Leone; Gulf of Guinea; *Tylosurus crocodilus* (gill chambers), Sarasota, Fla.; Virginia Key, Fla.; U.S. Atlantic Coast; Havana, Cuba; Golfo de Lanaio, Venezuela; Venezuela; Delagoa Bay, Mozambique; Kenya; Mosios Islands, Burma; Kerala, India; *Lhotskia gavialoides* (oral valves), Botany Bay, Australia;



FIGURES 65–73.—*Paraergasilus* and *Parabomolochus*. 65–70. *Paraergasilus remulus*, new species, female (continued). 65. Mandible. 66. First maxilla. 67. Second maxilla. 68. First leg. 69. Second leg. 70. Fourth leg. 71–72. *Parabomolochus bellones* (Burmeister), female. 71. Dorsal view. 72. Fifth leg. 73. *Parabomolochus ensiculus*, new species, female, dorsal view.

"Australia"; Great Barrier Reef; Newcastle, Australia; New South Wales, Australia.

Remarks.—This species has been reported many times in the literature. Vervoort (1962) provided a good description with figures of the female; little additional description is necessary here. He, however, described and figured the exopod of leg 1 as 2-segmented; all of our specimens show this ramus to be 3-segmented and similar to the figure of leg 1 provided in the description of the following species.

We tested the variability of one taxonomic character—the relative lengths of the spines and setae on leg 5—in our large series of collections from a wide range of hosts and localities. It was apparent that the spines and setae are of taxonomic importance and that their relative lengths vary in *Parabomolochus bellones* as well as in other species. This variation in the four species of *Parabomolochus* considered in this paper is discussed in a later section.

Parabomolochus ensiculus Cressey, New Species

Figures 73 to 86

Specimens studied.—A total of 153 individuals from 14 collections from under the oral valves of two species of eastern Pacific needlefish hosts: *Strongylura exilis*, San Diego, Calif. (2 collections); Baja California (3 collections); Chame Point, Panama (gill cavity); Pachacamac Island, Peru; Peru; *Strongylura scapularis*, Balboa, Panama (2 collections); Manabi Province, Ecuador; Guyaquil, Ecuador; Point Pizarro, Peru; Western South America.

Holotype female (USNM 125691), allotype male (USNM 125692), and 33 paratypes (29 females, 4 males) (USNM 125693) from the oral valves of 5 *Strongylura scapularis* (USNM 84276) collected at Balboa, Panama.

Female.—Body form as in figure 73. Total length and greatest width of three specimens: 1,420μ by 520μ, 1,270μ by 600μ, 1,195μ by 480μ. Body form in general like that of *P. bellones*. Thoracic segments not inflated dorsally, not overlapping succeeding segments. Genital segment and abdomen as in *P. bellones*, except for the patch of spinules present on the last abdominal segment of *P. ensiculus*. Caudal rami (fig. 74) armed with setae as in *P. bellones* but different from that species by the presence of a prominent patch of spinules on the ventral surface of the posterior third of the ramus; rami of three specimens measure 133μ by 57μ, 129μ by 58μ, and 119μ by 46μ; slightly more than twice as long as wide (in *P. bellones* the rami are less than twice as long as wide, 100μ by 58μ).

First antenna (fig. 75) armed as in figure. Second antenna (fig. 75) as in *P. bellones*. Oral area as in figure 76. Labrum surface with two patches of scalelike processes and fine fringe on lateral border. Mandible broad, bladelike with small accessory process at tip. Paragnath finger-shaped with row of fringe. First maxilla with three stout plumose setae and a shorter naked one. Second maxilla (fig. 77) with two distal processes; shorter plumose, longer with heavy fringe. Maxilliped (fig. 75) with prominent lateral tooth on outer border of terminal hook as in *P. bellones*.

Legs 1 to 4 biramose, all rami 3-segmented. Leg 1 (fig. 78) exopod first segment with broad spine on outer distal corner, surface of spine striated; remainder of leg armed with spines and setae as in figure. Leg 2 (fig. 79) as in *P. bellones* except last segment of exopod with three outer spines (*P. bellones* has four), bases of setae swollen on first two segments of endopod. Leg 3 (fig. 80) and leg 4 (fig. 81) as in *P. bellones* except terminal spine on exopod of both legs proportionally longer in *P. ensiculus* The spine and seta formulas for legs 1 to 4 follow:

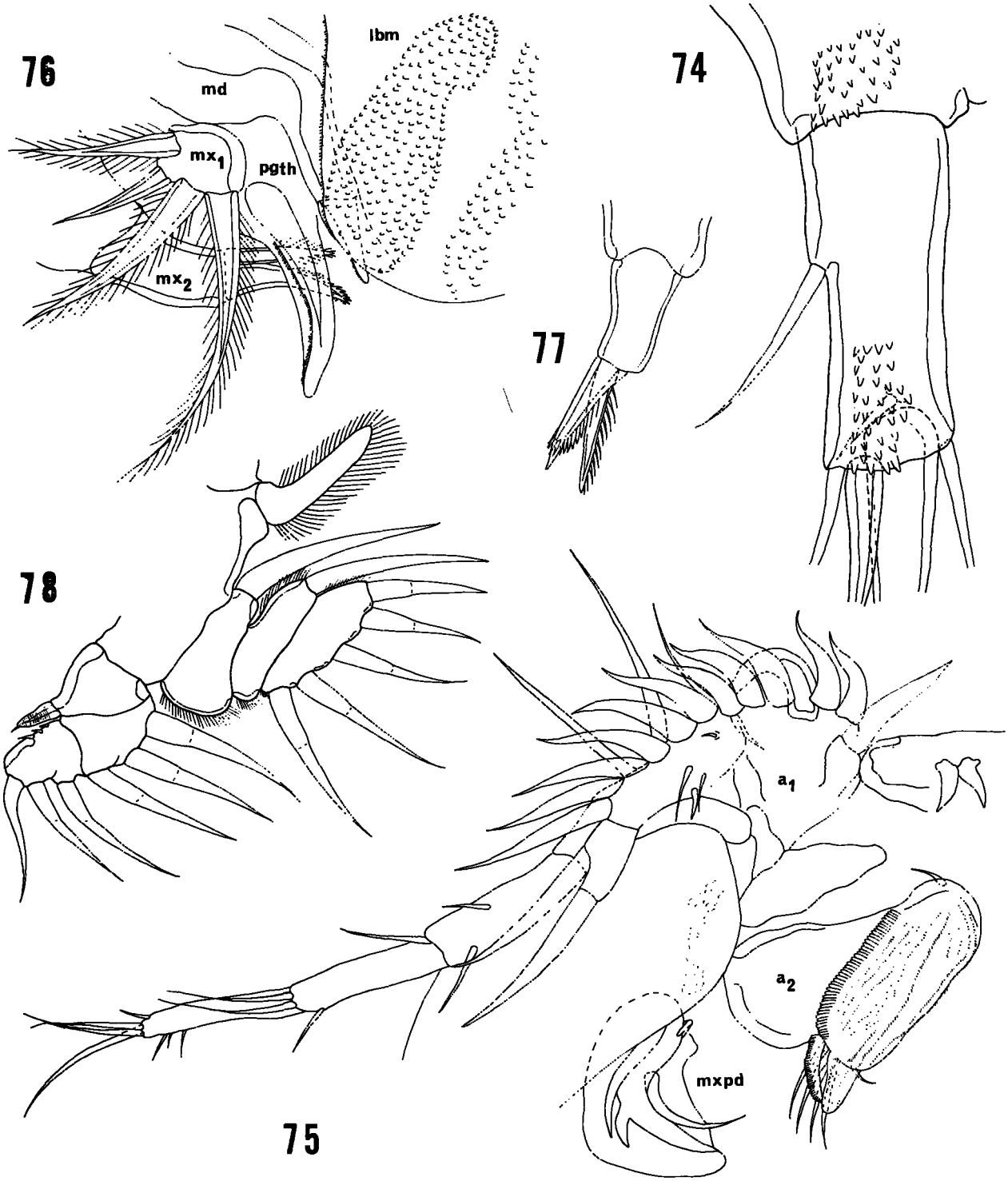
	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	I:0	0:1	I:0	0:1	I:0	0:1
Seg. 2	0:3	0:1	I:1	0:2	I:1	0:1	I:1	0:1
Seg. 3	III:3	5	III:5	II:3	III:5	II:2	III:4	I:1:I

Leg 5 (fig. 82) 2-segmented; terminal segment with an outer prominent spine, two terminal broad spines separated by a median terminal seta, and patches of setules near bases of spines as in figure. Leg 6 absent.

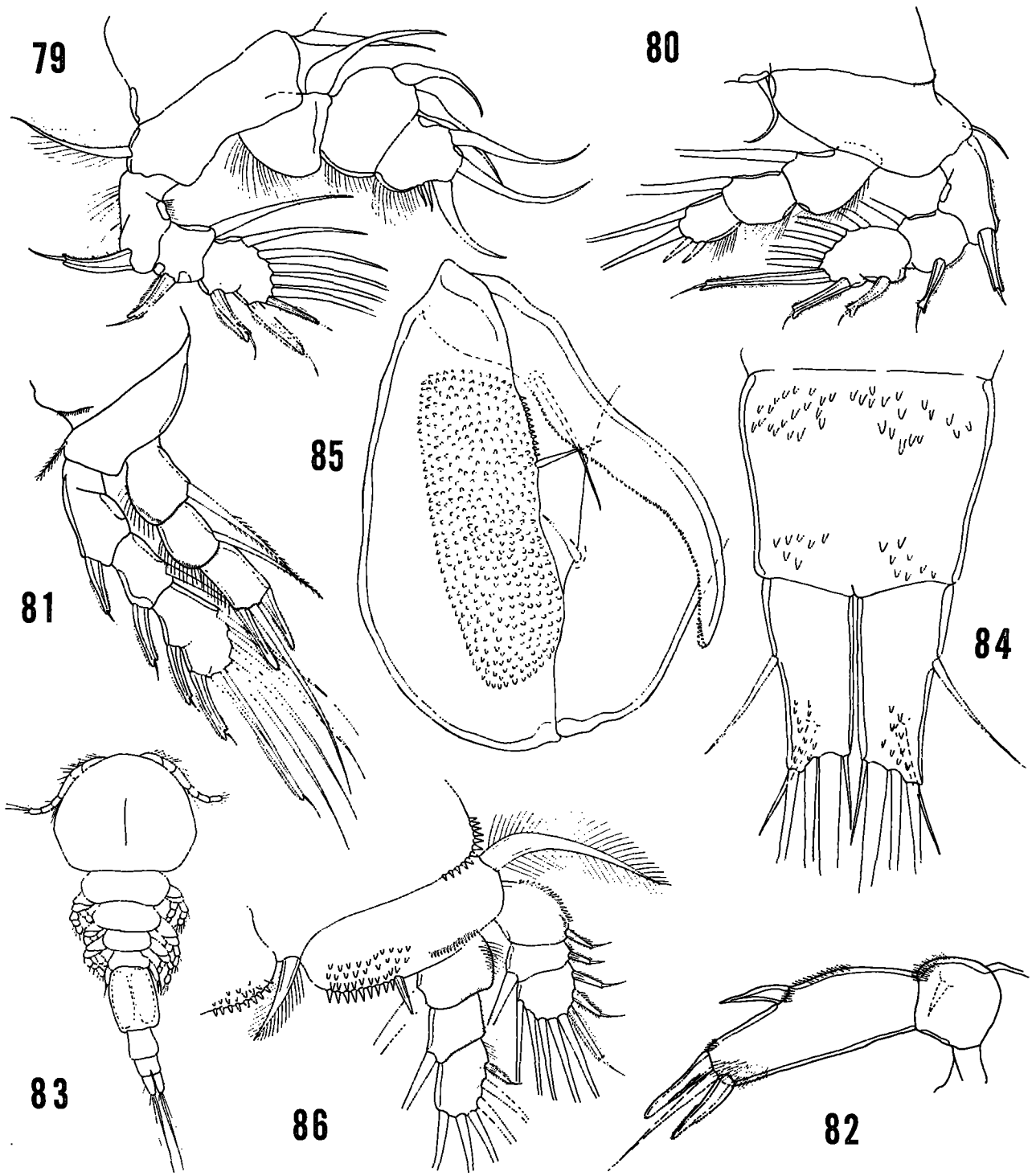
Egg sacs about 800 μ long, containing about 40 eggs.

Color in preserved specimens, cream.

Male.—Body form as in figure 83. Total length 1,116 μ. Greatest width 507 μ. Cephalon slightly wider than long (406 μ x 507 μ). Thoracic segments bearing legs 2 to 5 free, each narrower than the preceding segment. Similar to *P. bellones* in general body form. Last abdominal segment and caudal



FIGURES 74–78.—*Parabomolochus ensiculus*, new species, female (continued). 74. Caudal ramus, ventral view. 75. First antenna (a_1), second antenna (a_2), and maxilliped (mxpd). 76. Mouth parts (labrum, lbm; mandible, md; paragnath, pgth; first maxilla, mx_1; second maxilla, mx_2). 77. Tip of second maxilla. 78. First leg.



FIGURES 79–86.—*Parabomolochus ensiculus*, new species, female (continued). 79. Second leg. 80. Third leg. 81. Fourth leg. 82. Fifth leg. Same, male. 83. Dorsal view. 84. Caudal rami, ventral view. 85. Maxilliped. 86. First leg.

rami (fig. 84) with patches of broad spinules. Maxilliped (fig. 85) second segment with a large patch of spinules. Leg 1 (fig. 86) with patches of broad spinules on interpodal plate and basipod, otherwise armed as in *P. bellones*. Other appendages as in *P. bellones*.

Etymology.—The specific name *ensiculus*, Latin for "sword," refers to the terminal spines on the female 5th leg.

Remarks.—*P. ensiculus* can be separated from all other members of the genus by the spines on leg 5. This species is apparently restricted to the eastern Pacific Ocean and so far has been collected only from *Strongylura exilis* and *S. scapularis*, both hosts endemic to that area.

The male of this species can be separated from *P. bellones* only by the more prominent spinules on the interpodal plates, maxilliped, and basipod of leg 1 of *P. ensiculus*.

Parabomolochus constrictus Cressey, New Species

Figures 87 to 90

Specimens studied.—A total of 178 individuals from 32 collections from the gill chambers of 6 species of eastern Pacific needlefishes: *Ablennes hians*, Acapulco, Mexico; Panama Bay, Panama (2 collections); Ecuador; Cabo Blanco, Peru (2 collections); *Platybelone argalus*, Bahia Santa Maria, Baja California; Secas Island, Panama; Perlas Islands, Panama; Gulf of Panama; Galapagos Islands; Gulf of Guayaquil, Ecuador; *Strongylura scapularis*, Gulf of Nicoya, Costa Rica; Panama Canal Zone (3 collections); *Strongylura exilis*, Baja California (5 collections); Gulf of California; northern Peru; *Tylosurus acus*, Costa Rica (2 collections); Panama (2 collections); Colombia; Cabo Blanco, Peru; *Tylosurus crocodilus*, Tangola, Mexico; Cocos Islands; Panama (2 collections).

Holotype female (USNM 125694) and 43 paratype females (USNM 125695) from 13 specimens of *Platybelone argalus pterura* from the Gulf of Guayaquil, Ecuador.

Female.—Body form as in *P. ensiculus*. Total lengths and greatest widths of three specimens: 1,050 μ by 600 μ, 1,050 μ by 600 μ, 980 μ by 560 μ. Patches of fine spinules present on ventral surface of last abdominal segment and caudal rami (fig. 87). Caudal rami proportionally larger than in *P. ensiculus* and *P. bellones;* lengths and widths of the rami of three specimens are 152 μ by 74 μ, 143 μ by 73 μ, and 138 μ by 80 μ.

Cephalic appendages as in *P. ensiculus* with following exceptions: paragnath bladelike with fringe along posterior border and encircling tip; second maxilla (fig. 89) largest terminal spine with large patch of spinules, smaller spine with prominent spines on both edges; maxilliped (fig. 88) with small, blunt lateral tooth on outer border as compared to prominent pointed tooth present in both *P. bellones* and *P. ensiculus*. Surface of labrum with two patches of fine spinules.

Legs 1 to 4 as in *P. ensiculus*. Leg 5 (fig. 90) outer two spines on terminal segment pinched near tip; inner spine pinched near midpoint, distal half narrowed. Patches of spinules near bases of spines with finer spinules than those of *P. ensiculus*. Leg 6 absent.

Egg sacs as in *P. ensiculus*.

Color in preserved specimens, cream.

Male.—Unknown.

Etymology.—The specific name *constrictus* is Latin for "drawn together" and refers to the nature of the spines on the 5th leg of the female.

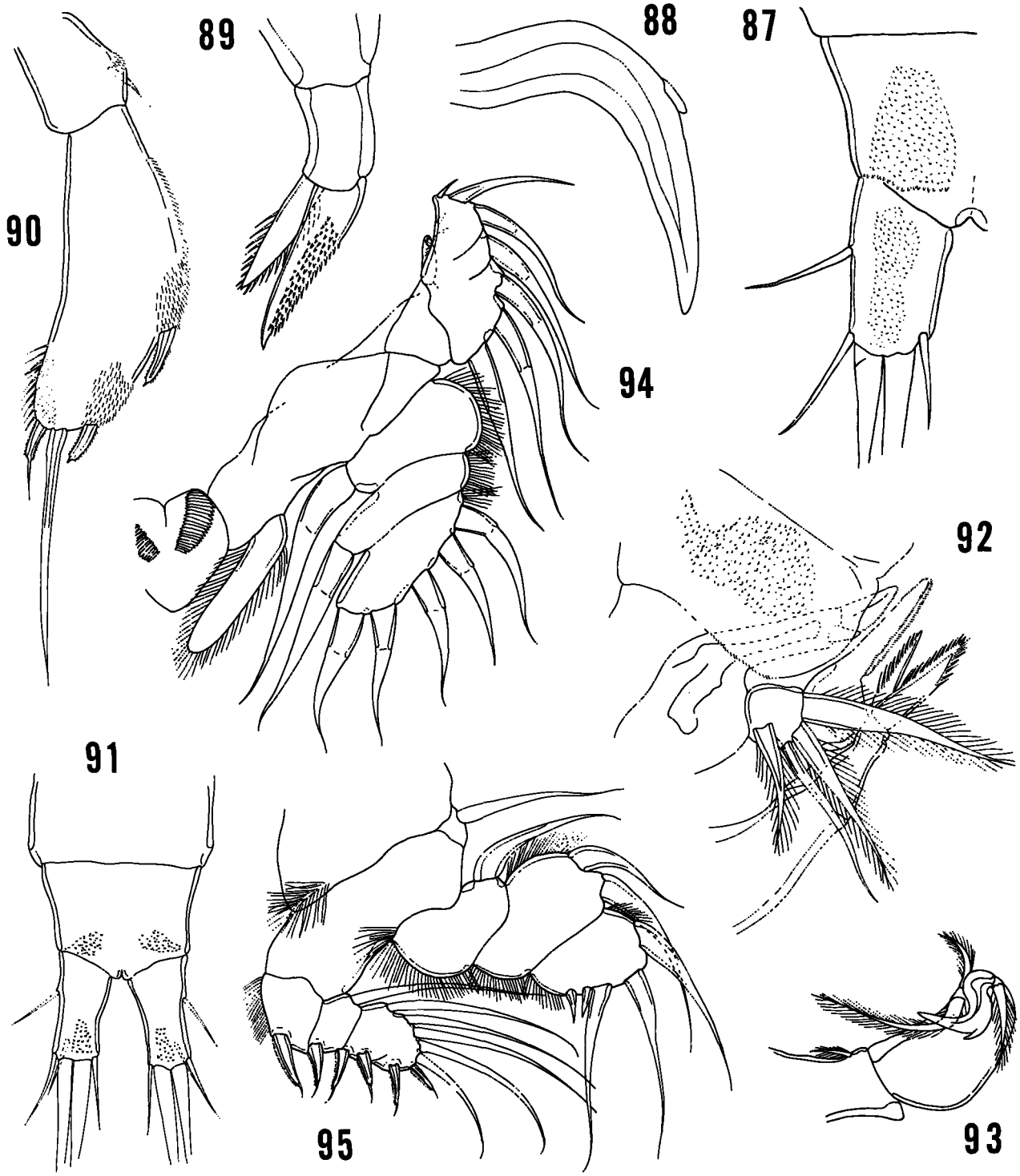
Remarks.—This species can be separated from all other known members of the genus by the nature of the 5th leg spines. It is described here from five species of needlefishes and is apparently endemic to the eastern Pacific Ocean.

Subsequent to this study, Cressey examined parasitic copepods collected by Edmund Hobson at La Jolla, Calif., from 30 species of inshore fishes. *Parabomolochus constrictus* was collected from one collection of each of the following hosts: Atherinidae, *Atherinops affinis* (Ayres); and Embiotocidae, *Micrometrus minimus* (Gibbons), *Phanerodon atripes* (Jordan and Gilbert), and *Rhacochilus vacca* (Girard). These additional hosts point out the "loose" host specificity in this species, and it is likely that bomolochids as a group are less host specific than most other parasitic copepods. In each of the California collections, only one copepod was collected from each individual.

Parabomolochus sinensis Cressey, New Species

Figures 91 to 98

Specimens studied.—Six collections containing 12 females and 1 male from the oral valves of *Strongylura strongylura* and a single collection containing 2 females from the upper oral valve of



FIGURES 87–95.—*Parabomolochus*. 87–90. *P. constrictus*, new species, female. 87. Caudal ramus, ventral view. 88. Claw of maxilliped. 89. Tip of second maxilla. 90. Fifth leg. 91–95. *P. sinensis*, new species, female. 91. Caudal rami, ventral view. 92. Mouth parts. 93. Maxilliped. 94. First leg. 95. Second leg.

Ablennes hians as follows: *Ablennes hians*, Batavia, Java; *Strongylura strongylura*, Fukien, China; Hong Kong (2 collections); Amoy, China (2 collections); Penang, Malaysia.

Holotype female (USNM 125696) and two paratype females (USNM 125697) from the oral valves of a *Strongylura strongylura* (ANSP 76986) from Hong Kong.

Female.—Body form as in *P. ensiculus*. Total length 2,100 μ. Greatest width 1,100 μ. Thoracic segments not inflated dorsally, not overlapping succeeding segments. Genital segment wider than long (207 μ by 325 μ). Abdomen 3-segmented; lengths of segments from anterior to posterior 106 μ, 65 μ, and 83 μ, respectively, last segment with ventral patches of spinules (see fig. 91) near outer distal corners (spinules not as conspicuous as in *P. ensiculus*). Caudal rami (fig. 91) about twice as long as wide (75 μ by 34 μ, 65 μ by 31 μ, 65 μ by 35 μ for three specimens); each with a ventral patch of spinules as indicated in figure.

First and second antennae as in *P. ensiculus*. Oral area as in figure 92; labrum with a patch of scalelike processes on each half (finer than those of *P. ensiculus*). Mandible with two terminal processes, inner process much shorter than outer. Paragnath bladelike, double row of fringe along posterior border. First maxilla with four long setae—three plumose, one naked. Second maxilla as in *P. ensiculus*. Maxilliped (fig. 93) with accessory process on claw; terminal segment with three plumose setae.

Legs 1 to 4 biramose, all rami (except leg 1 exopod) 3-segmented and all setae plumose. Leg 1 (fig. 94) exopod first segment with broad spine on outer distal corner, second segment with three small outer spines and six well-developed setae; endopod 3-segmented, first two segments each with an inner seta and terminal segment with five setae. Leg 2 (fig. 95) exopod, first segment with an outer spine, second segment with an outer spine and an inner seta, terminal segment with four outer spines (*P. ensiculus* has three) and five terminal to inner setae; endopod, first segment with an inner seta, second segment with two inner setae, terminal segment with two short outer spines and three terminal setae. Leg 3 (fig. 96) exopod, first two segments armed as in leg 2, terminal segment with three outer spines and five terminal to inner setae; endopod, first two segments each with an inner seta, terminal segment with two terminal setae and two short outer spines. Leg 4 (fig. 97) exopod, first two segments armed as in legs 2 and 3, last segment with three outer spines (terminal-most about twice the length of other two) and four terminal to inner setae; endopod, first two segments armed as in leg 3, last segment with an inner and an outer spine and a median terminal seta. Spine and seta formulas of legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	I:0	0:1	I:0	0:1	I:0	0:1
Seg. 2	III:6	0:1	I:1	0:2	I:1	0:1	I:1	0:1
Seg. 3	-----	5	IV:5	II:3	III:5	II:2	III:4	I:1:I

Leg 5 (fig. 98) armed as in *P. ensiculus;* ratio of seta 1 to seta 2 less than in *P. bellones* or *P. ensiculus* (see Discussion). Leg 6 represented as two setae on lateral border of genital segment.

Egg sacs broken in the only specimens bearing them.

Color in preserved material, cream.

Male.—Unknown.

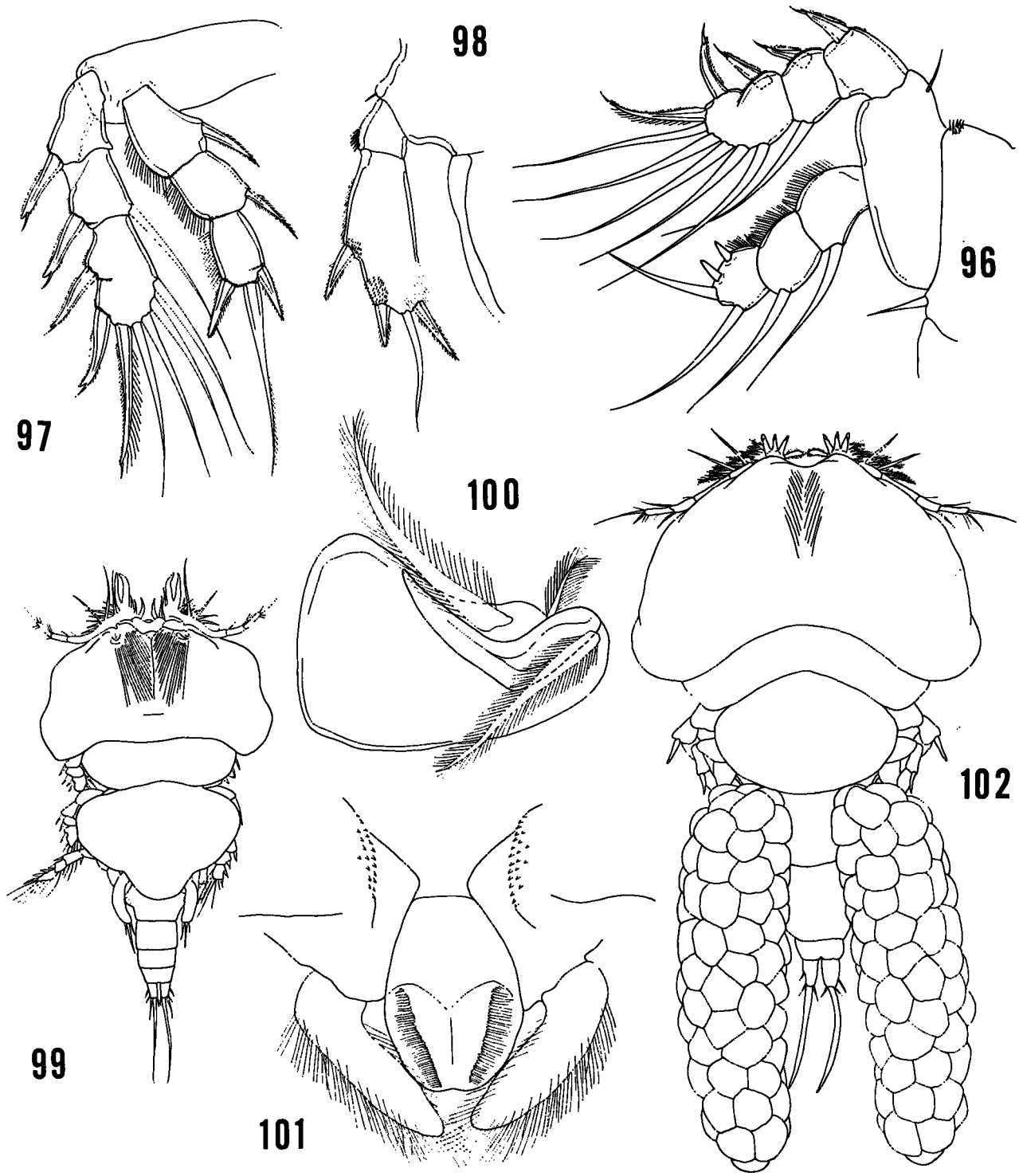
Etymology.—The specific name *sinensis* refers to the geographic area (China coast and environs) to which this species seems to be restricted.

Remarks.—This species can be separated from all species of the genus except *P. ensiculus*, *P. constrictus*, and *P. decapteri* Yamaguti by the patches of spinules on the ventral surface of the caudal rami and last abdominal segment. It can be separated from *P. constrictus* by the nature of the setae of leg 5. *P. ensiculus* has only three spines on the last exopod segment of leg 2, whereas *P. sinensis* has four; also the spinules on the caudal rami, abdomen, and labrum are much heavier in *P. ensiculus*. Finally, *P. sinensis* can be separated from *P. decapteri* by the presence of patches of spinules on the exopod segments of legs 2 to 4 of *P. decapteri* and their absence in *P. sinensis*.

***Nothobomolochus gibber* (Shiino)**

Figures 99 to 101

Specimens studied.—A total of 235 females from 20 collections from 6 species of hosts. From the Mediterranean and eastern Atlantic, collections were made from the following hosts and localities: *Belone belone*, Funchal, Madeira; *Belone svetovidovi*, Tunisia; Genoa, Italy; *Platybelone argalus*, Ascension and Annobon Islands, Gulf of Guinea. From the Indo-West Pacific, collections were made from the following hosts and localities: *Ablennes*



FIGURES 96–102.—*Parabomolochus* and *Nothobomolochus* species. 96–98. *P. sinensis*, new species, female (continued). 96. Third leg. 97. Fourth leg. 98. Fifth leg. 99–101. *N. gibber* (Shiino), female. 99. Dorsal view. 100. Maxilliped. 101. Area between coxopods of leg 1. 102. *N. digitatus*, new species, female, dorsal view.

hians, Andaman Islands, Bay of Bengal; Borneo; Torres Strait, northern Australia; Manila, Philippine Islands; Japan (2 collections); *Platybelone argalus*, Aldabra Island, Indian Ocean; Marshall Islands (4 collections); Tokelau Islands (2 collections); Fakaofo Atoll (2 collections); Christmas Island; Line Islands; Fanning Island; Rose Island, Samoan Islands; Apia, Samoa (2 collections); *Tylosurus acus*, Taiwan; *Tylosurus crocodilus*, Red Sea; Zanzibar; Seychelles Islands; Nosy Bé, Madagascar; Kerala, India; Cavite, Philippine Islands; Bellona Island, British Solomon Islands.

Female.—Body form as in figure 99 (after Shiino, 1957). This species was well described by Shiino (as *Bomolochus gibber*) in 1957, and additional notes were provided by Vervoort in 1962. No additional description is necessary here except to point out two characters not considered by the aforementioned authors which may have some taxonomic value: the maxilliped (fig. 100) terminal claw is angular, the distal half nearly at a right angle to the base, and the area between the coxopods of leg 1 (fig. 101) has a pad with surface corrugations as indicated in figure.

Remarks.—This species is common in the Indo-Pacific region and only occasionally found in the Mediterranean and eastern Atlantic.

***Nothobomolochus digitatus* Cressey, New Species**

Figures 102 to 112

Specimens studied.—Fourteen collections containing 28 females from four species of needlefishes, all from the Indo-West Pacific area as follows: *Strongylura leiura*, Gulf of Thailand; Panay, Philippines (2 collections); Java; *Strongylura strongylura*, Calicut, India; Bombay, India (3 collections); Malaysia (2 collections); Hong Kong; Australia; Philippines; *Tylosurus crocodilus*, British North Borneo; *Tylosurus punctulatus*, New Guinea.

Holotype female (USNM 125698) and two paratype females (USNM 125699) from a specimen of *Strongylura strongylura* (SU 32879) from Penang, Malaysia.

Female.—Body form as in figure 102. Total length 1,800 μ. Greatest width 1,200 μ. Caudal rami (fig. 103) longer than wide (66 μ by 44 μ) with one long terminal seta (413 μ), three subterminal short setae, and one lateral seta. First antenna (fig. 104) with three stout, modified setae of equal length on basal segment; each seta with a hyaline tip, other setae as in other members of the genus. Second antenna as in *P. gibber*. Labrum (fig. 105) with two rings of blunt spinules on surface. Mandible (fig. 106) terminating in two short bladelike processes, each with a fringe along one edge. Paragnath (fig. 107) with nine fingerlike terminal processes, each with a bulbous tip. In view of the striking difference between the paragnaths of *gibber* and *digitatus* this structure is of great interest and taxonomic importance. First maxilla (fig. 108) bearing three long plumose setae and a shorter naked one. Second maxilla (fig. 109) ending as a long bladelike process with a stout basal seta. Arrangement of mouth parts as in figure 105. Maxilliped (fig. 110) with terminal claw slightly recurved, not angular. Area between coxopods of leg 1 (fig. 111) with wreathlike fringe as in figure.

Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	III:6	0:1	I:0	0:1	I:0	0:1	I:0	0:1
Seg. 2	-----	0:1	I:1	0:2	I:1	0:1	I:1	0:0
Seg. 3	-----	5	IV:5	II:3	III:5	II:2	III:4	I:1:I

Leg 5 (fig. 112) similar to that of other members of the genus; two outer terminal spines with very fine spinules on inner margin, patch of spinules near base of terminal spines heavier than in *N. gibber*. Leg 6 absent.

Egg sacs about 1 mm. long and containing 60 to 75 eggs.

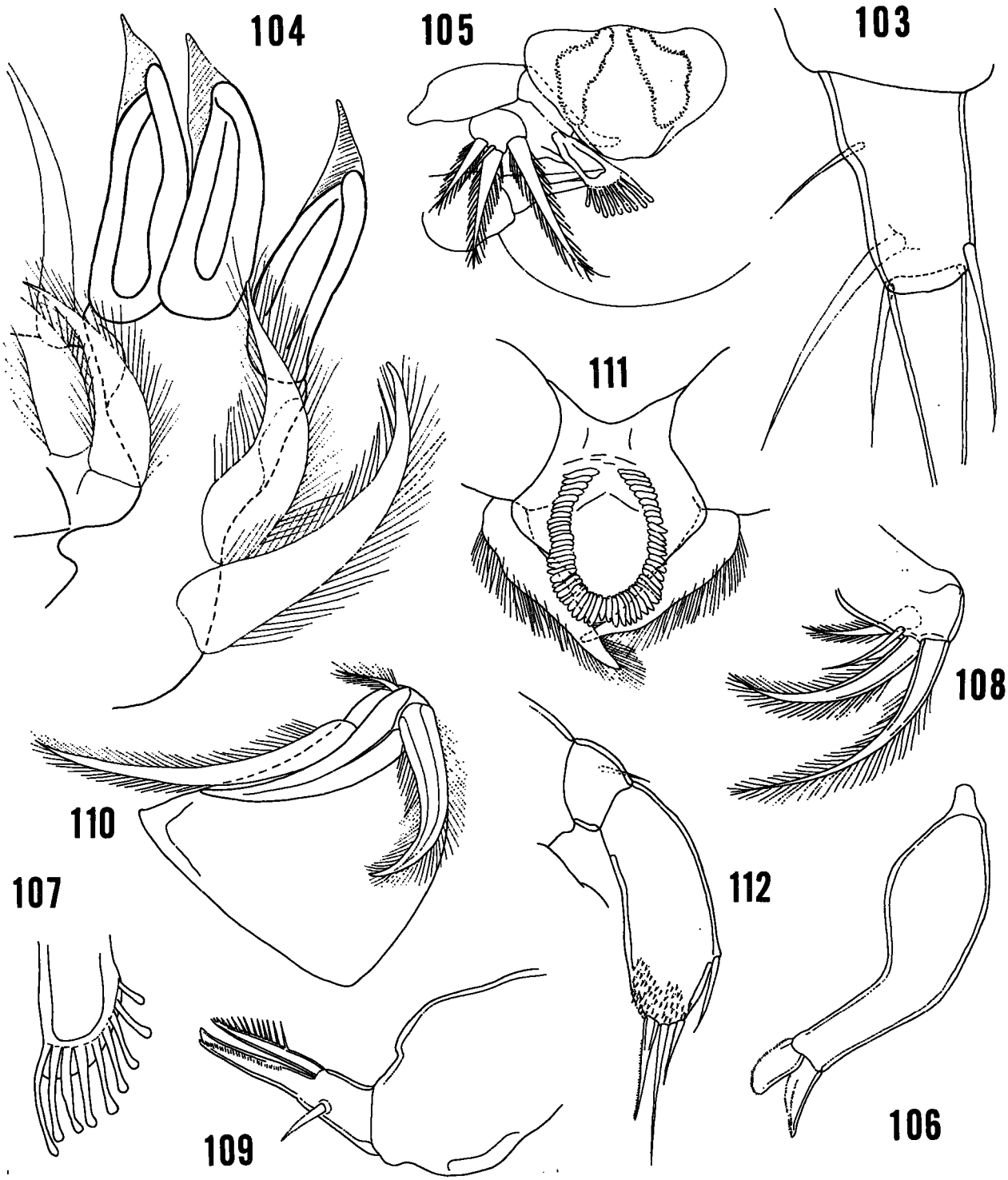
Color in preserved specimens, cream.

Male.—Unknown.

Etymology.—The word *digitatus* refers to the fingerlike processes on the paragnath.

Remarks.—This species can be separated from all other species except *N. saetiger* (Wilson) and *N. lateolabricus* (Yamaguti and Yamasu) by the nature of the first antenna: the three modified spines on the first segment are of equal length, whereas in all other species they are not. The new species can be separated from *N. saetiger* and *N. lateolabricus* by the nature of the paragnath. In *N. saetiger* and *N. lateolabricus* the paragnath is a bladelike structure, whereas in *N. digitatus* it bears nine fingerlike processes at its distal end.

This species is known only from Indo-West Pacific needlefishes.



FIGURES 103–112.—*Nothobomolochus digitatus*, new species, female (continued). 103. Caudal ramus, ventral view. 104. Base of first antenna. 105. Mouth parts. 106. Mandible. 107. Paragnath. 108. First maxilla. 109. Second maxilla. 110. Maxilliped. 111. Area between coxopods of leg 1. 112. Fifth leg.

Order Caligidea

Four families of caligoid copepods were collected from needlefishes: Caligidae, Anthosomatidae, Lernaeidae, and Lernaeoceridae.

FAMILY CALIGIDAE

Seven species of *Caligus* plus *Caligodes laciniatus* were collected.

Caligus tylosuri (Rangnekar)

Figures 113 to 116

Specimens studied.—Two collections from *Tylosurus crocodilus*, one from Leyte, Philippines, containing three females and one from North Borneo containing a single female; one collection from *Tylosurus acus melanotus* from Luzon, Philippines, containing a single male and one collection from *T. acus pacificus* from Bahia Palmas, Gulf of California, containing a single male.

This copepod was described by Rangnekar in 1956 and at that time assigned to the genus *Tuxophorus*. In 1961 Pillai transferred it to the genus *Caligus*. Rangnekar's primary reason for placing this copepod in *Tuxophorus* was the presence of small dorsal thoracic plates which she described from females in her collections. Pillai was unable to find these plates in his material and, thus, reassigned the species to *Caligus*. These plates could not be located on the specimens reported here.

This copepod has been described and figured by Rangnekar and Pillai so only a few points are added to the existing descriptions.

Female.—Body form as in figure 113. Total length and greatest width of the specimen from North Borneo 3.7 by 2.1 mm.; those from Leyte, Philippines 3.3 by 2.0 mm., 3.4 by 2.0 mm., and 3.5 by 2.1 mm.

Male.—Body form as in figure 114. Total length and greatest width of the specimen from Luzon, Philippines, 3.2 by 1.9 mm.; those from Gulf of California 2.9 by 1.7 mm. Abdomen (fig. 115) 2-segmented (not 1-segmented as stated by Rangnekar). Caudal rami (fig. 116) with six setae arranged as in figure.

The following points concerning the description should be corrected as follows. Rangnekar described the endopod of leg 3 as 2-segmented and stated "exo and endopods are well separated by a ciliated membrane." This "membrane" is actually the first endopod segment, thus the endopod is 3-segmented. The 5th and 6th legs described by Rangnekar are parts of leg 5—the anterior lobe represents the exopod and the posterior lobe the endopod. Leg 6 is represented by a single seta near the junction of the genital segment and abdomen.

Remarks.—This copepod seems to be restricted to needlefishes. It has thus far not been reported from the Atlantic Ocean.

Caligus belones Krøyer

Figure 117

Specimens studied.—A single collection containing 1 female from under the gill cover of a *Belone belone* taken in the Elbe River plus the type-specimens from *B. vulgaris* (=*B. belone*) borrowed from the Universitetets Zoologiske Museum (Copenhagen). A lectotype has been selected and deposited in the above museum. An additional collection from *P. argalus* containing 1 female and 1 male.

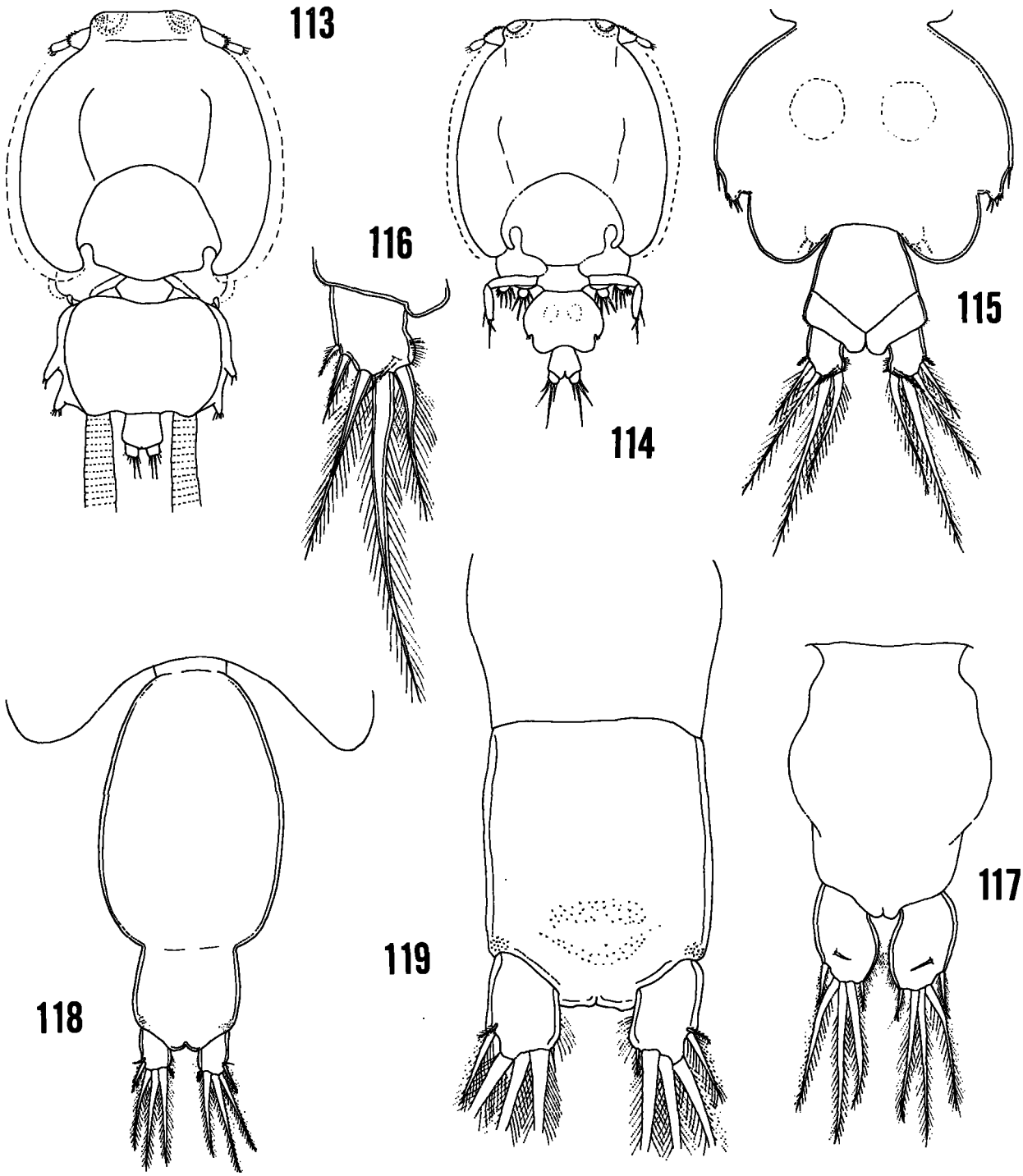
Total length and greatest width 5.7 by 2.1 mm. Abdomen (fig. 117) 1.1 mm. long and 1-segmented. Caudal rami large (384 μ by 266 μ), longer than wide; outermost of three longest setae bent inwardly, longest seta 650 μ long. Sternal furca spatulate, tines short. Leg 2 endopod with large patch of hairs on outer distal corner of first segment, rows of hairs on outer edge of second segment, small patch of hairs on third segment near junction of second and third segment. Leg 4 exopod 2-segmented with lateral spine and three terminal spines. Measurements of *B. belone* specimen.

The specimens assigned to *C. belones* from the dolphin *Coryphaena equisetis* by Wilson (1905) were described as a new species (*C. wilsoni*) by Delamare Deboutteville and Nuñes-Ruivo in 1958.

Caligus malabaricus Pillai

Figure 118

Specimens studied.—Two collections containing five females from *Ablennes hians* from Torres Strait off Northern Australia. Total length and greatest width of the specimens 4.13 by 1.42 mm., 4.13 by 1.35 mm., 3.90 by 1.27 mm., 3.75 by 1.35 mm., and 3.60 by 1.35 mm. In the largest specimen the genital segment is 1.27 by 1.12 mm. (longer than wide). The abdomen in this same specimen is 1.35 mm. long. Pillai (1961) provided a description with good figures of this species which he reported from *Tylosurus crocodilus* from India. In addition to his description it should be noted that the abdomen has a patch of spinules on the posterior corners as indicated in figure 118.



FIGURES 113–119.—*Caligus* species. 113–116. *C. tylosuri* (Rangnekar). 113. Female, dorsal view. 114. Male, dorsal view. 115. Female, genital segment and abdomen, ventral view. 116. Female, caudal ramus, ventral view. 117. *C. belones* Krøyer, female, abdomen and caudal rami, ventral view. 118. *C. malabaricus* Pillai, female, abdomen and caudal rami, ventral view. 119. *Caligus* species A, female, last abdominal segment and caudal rami, ventral view.

***Caligus* Species A to D**

Figures 119 to 132, Plate 1

In addition to the three species of *Caligus* reported above, the collections of copepods from needlefishes included four additional species of *Caligus*. These collections generally contained only one or two specimens of each species. Robert Parker, Fisheries Research Board of Canada, is currently revising the genus *Caligus*, and in view of his work we have not attempted to assign names, new or otherwise, to these remaining four species. Information is included here which may facilitate determination of the status of these species when the genus is better understood.

Caligus sp. A.—Four collections containing six females from the Gulf of Guinea, three from *Ablennes hians* and one from *Tylosurus acus*. Total length and greatest width 3.8 by 1.7 mm. Abdomen 2-segmented, posterior segment (fig. 119) with fine spinules on outer ventral corners and a patch on the medial-ventral surface as in figure. Caudal ramus 207 μ long and 124 μ wide, middle seta of longest three is 475 μ long. Sternal furca (figs. 120 and 121) spatulate, tines of furca (fig. 120) more divergent in specimen from *T. acus* than in those (fig. 121) from *A. hians*. Leg 2 endopod (fig. 122) with patch of six stout spines on outer distal corner of first segment, rows of stout, distally bent spines on outer border of second segment, and a few small spines near outer junction of second and third segments on third segment. Leg 4 exopod (fig. 123) 2-segmented; terminal segment 366 μ long with lateral spine 118 μ long, three terminal spines measure 242 μ, 148 μ, and 88 μ from innermost to outermost.

Caligus sp. B.—One collection containing four females from *Strongylura notata* from Sarasota, Fla., and another collection containing one female from *Tylosurus acus pacificus* from Cabo Blanco, Peru. Total length and greatest width of Florida specimen 3.8 by 1.9 mm. Total length and greatest width of Peru specimen 4.7 by 2.1 mm. Abdomen (fig. 124) 1-segmented, unornamented. Caudal rami longer than wide 324 μ by 236 μ; longest seta 680 μ. Sternal furca (fig. 125) spatulate. Leg 2 endopod (fig. 126) with patch of hairs on outer distal corner of first segment, rows of hairs on outer edge of second segment, and a patch of hairs on third segment. Leg 4 (fig. 127) exopod 2-segmented; terminal segment with no lateral spine, three terminal spines 254 μ, 195 μ, and 116 μ, respectively, each with a prominent basal hood.

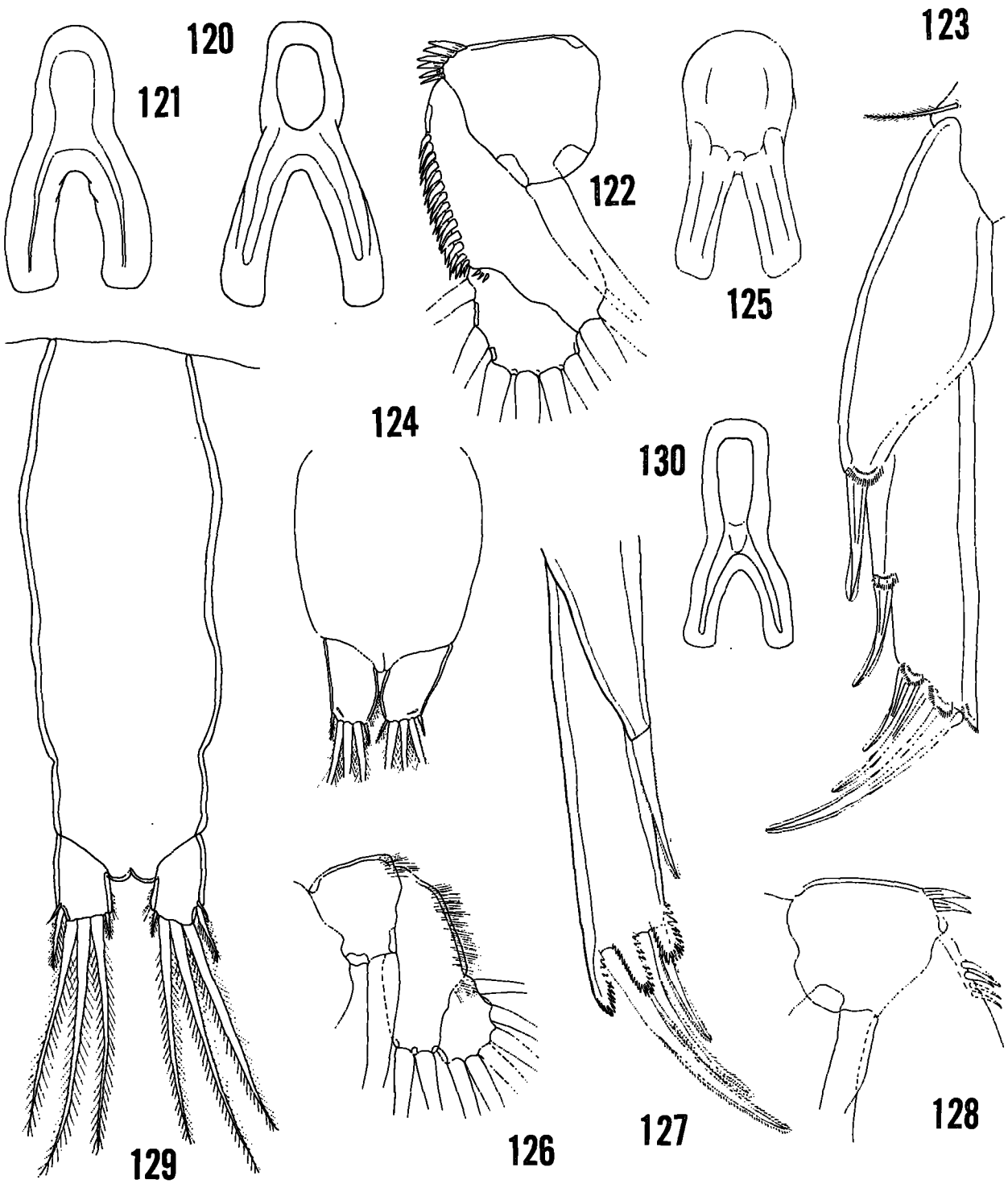
Caligus sp. C.—Two collections containing three females from *Tylosurus acus pacificus* and *T. crocodilus fodiator* from the Pacific side of Panama. Total length and greatest width 3.5 by 1.3 mm. This copepod is similar to *Caligus* sp. A in most respects including the presence of spinules on the ventral surface of the last abdominal segment. It differs from sp. A, however, in having only two prominent spines on the outer distal corner of the first endopod segment of leg 2 (fig. 128).

Caligus sp. D.—Two collections from the Philippines from *Strongylura incisa* and *S. urvillii*, each containing one female and a single collection containing one female from *Tylosurus choram* from the Red Sea. Total length and greatest width of specimen from *S. incisa*, 7.7 by 3.1 mm. Abdomen (fig. 129) 1-segmented and unarmed. Caudal rami small, slightly longer than wide (189 μ by 165 μ), longest seta 502 μ. Sternal furca (fig. 130) spatulate. Endopod of leg 2 (fig. 131) with patch of thin spines on outer corner of first segment, a row of thin spines along outer margin of second segment, and a few thin spines on third segment near outer basal corner. Leg 4 (fig. 132) exopod 2-segmented; terminal segment with a lateral spine, longest terminal spine about twice length of each of other two (230 μ).

***Caligodes laciniatus* (Krøyer)**

Figures 133 to 145, Plate 2

Specimens studied.—A total of 374 individuals from 94 collections from 7 host species. The host and locality data are provided below: *Ablennes hians*, off Pensacola, Fla.; Florida Keys; Padre Bank, Caribbean Sea; off Mississippi coast; off Surinam; off northern Brazil; Cape Verde Islands (2 collections); Gulf of Guinea (5 collections); off Sierra Leone (2 collections); Angola; Mauritius; Zanzibar; Japan (2 collections); Hawaii; off western Mexico (3 collections); off Peru (2 collections); *Strongylura leiura*, off Pondicherry, India; off Formosa; Philippines (3 collections); *Platybelone argalus*, Maldive Islands; *Lhotskia gavialoides*, off northern Australia (5 collections); *Tylosurus acus*, off southeast United States (5 collections); Gulf of Mexico (7 collections); Haiti; Virgin Islands; Gulf of Guinea; off Angola (2 collections); Philippines (4 collections); Japan;



FIGURES 120–130.—*Caligus* species. 120–123. *Caligus* species A, female (continued). 120. Sternal furca. 121. Sternal furca. 122. Endopod of second leg. 123. Fourth leg. 124–127. *Caligus* species B, female. 124. Abdomen and caudal rami, ventral view. 125. Sternal furca. 126. Endopod of second leg. 127. Last segment of fourth leg. 128. *Caligus* species C, female, first segment of second leg endopod. 129–130. *Caligus* species D, female. 129. Abdomen and caudal rami, ventral view. 130. Sternal furca.

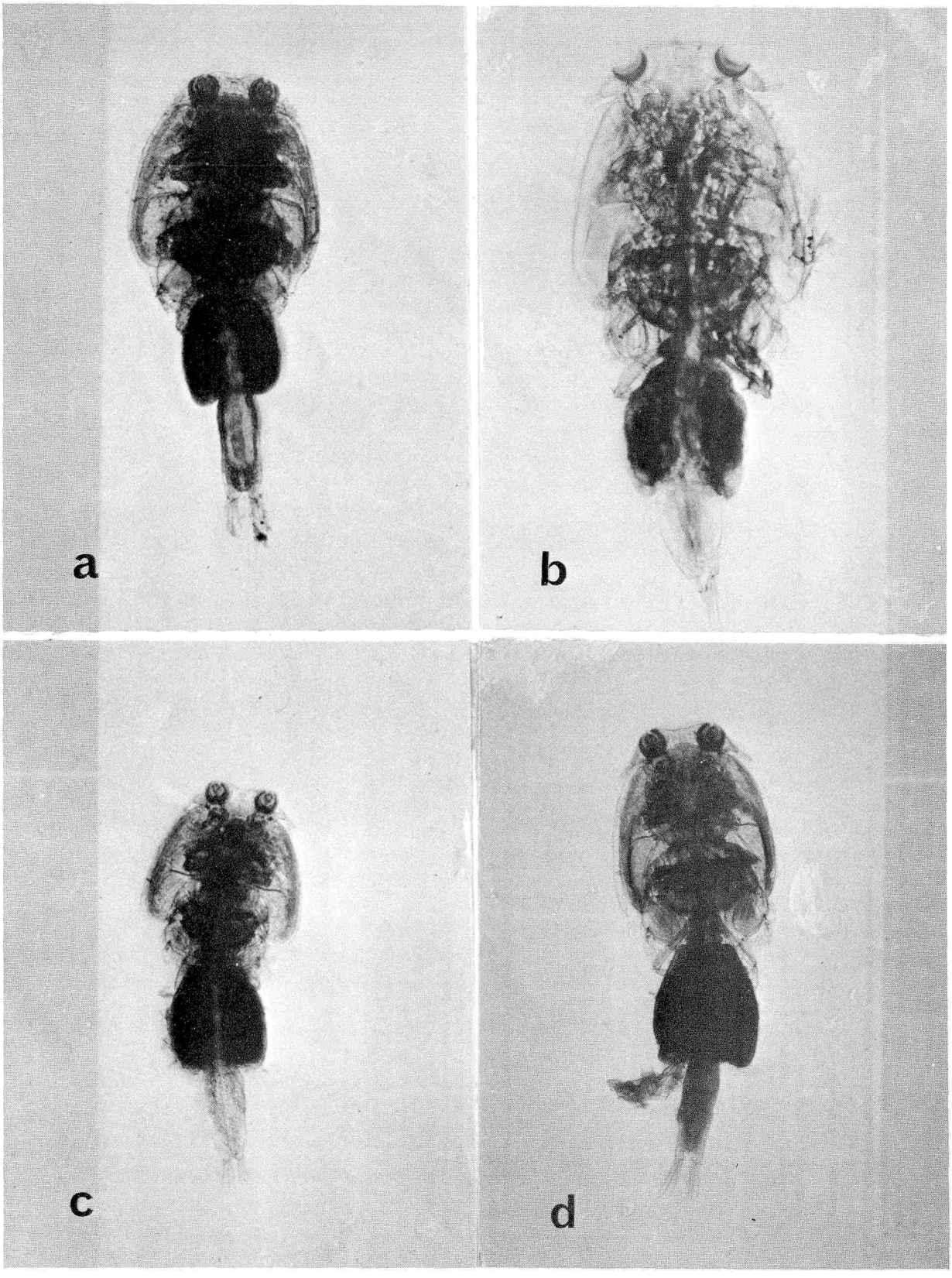


PLATE 1.—a. *Caligus* species A, female. b. *Caligus* species B, female. c. *Caligus* species C, female. d. *Caligus* species D, female.

Hawaii; Revillagigedos Islands, Mexico; Panama (Pacific); *Tylosurus crocodilus*, Matecumbe Key, Fla.; Cuba; Jamaica; Trinidad; off Venezuela; off Liberia; Gulf of Aden; Red Sea; off Zanzibar (2 collections); off Malagasy Republic (3 collections); Farquahar Island; Comores Islands; Aldabra Island; Mauritius; Seychelles Islands; Arabian Gulf; Ceylon; Madras, India; Singapore; Gulf of Thailand; Philippines; Samoa; Hawaii (2 collections); off west coast of Mexico (2 collections); off west coast of Panama; Cocos Islands (eastern Pacific); *Tylosurus choram*, Red Sea; Seychelles Islands.

Female.—Body form as in plate 2. Specimens examined had total lengths of 2.3 to 7.1 mm. (see Remarks). Greatest width in area of genital segment also varies but generally is not less than one-fourth or more than one-third of total length. In a form as variable as this, measurements of absolute size are not a reliable taxonomic character. Cephalon caligiform, about as wide as long. Lunules present. Thoracic segment bearing fourth legs free and in the form of a neck. Genital segment prominent, each posterior corner of segment has a long process that may or may not extend beyond end of abdomen. Abdomen 1-segmented, variable in length, and 5 to 7 times as long as wide. Caudal rami (fig. 133) small, bearing six setae, outermost and innermost naked, other plumose.

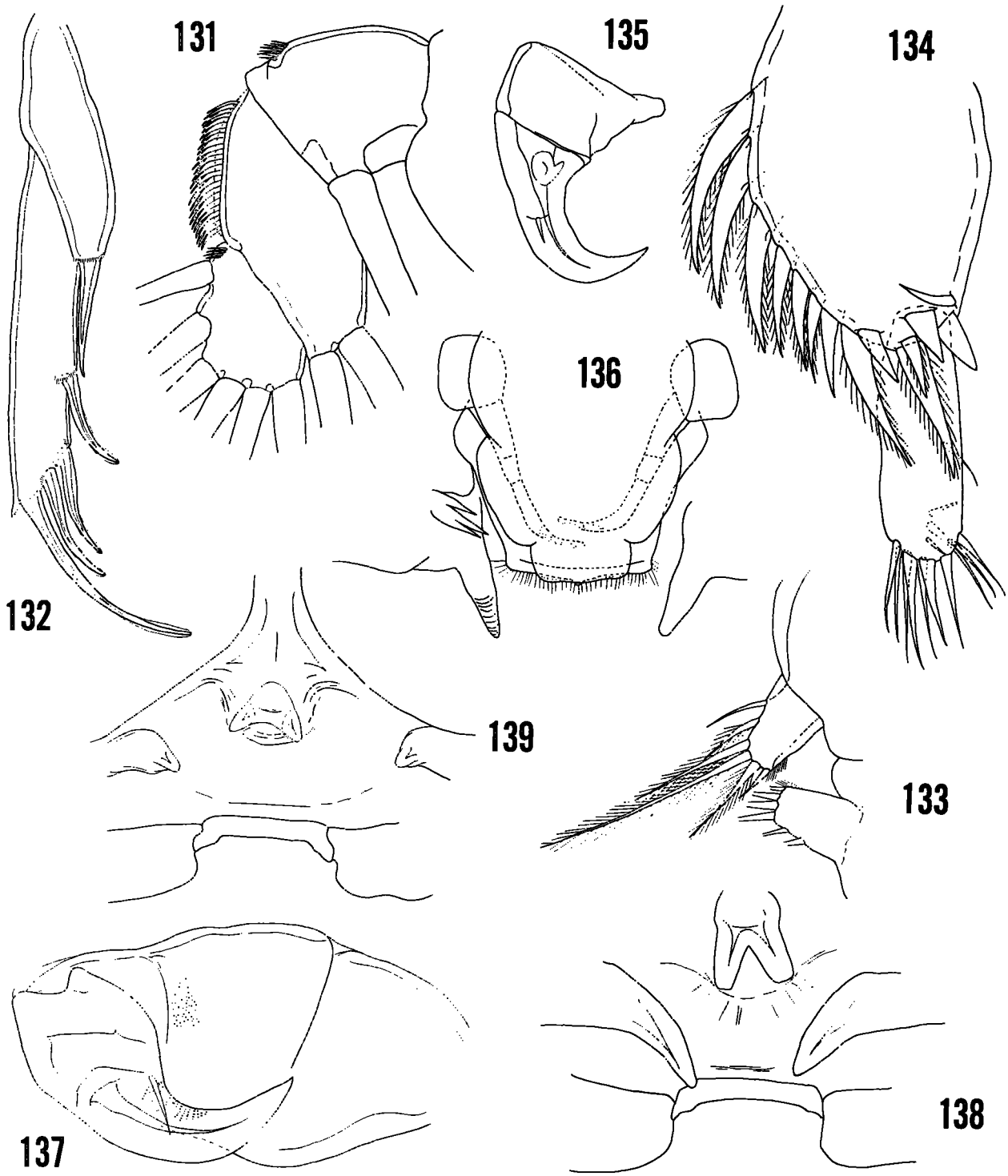
First antenna 2-segmented, armed with spines and setae as in figure 134. Second antenna (fig. 135) in form of a hook; terminal hook with two medium setae and accessory hooklike process near base. Mouthtube, mandible, and first maxilla (fig. 136) of usual caligoid form; first maxilla with three setae. Postoral processes present (fig. 136). Second maxilla of usual caligoid form, terminating in two plumose setae. Maxilliped (fig. 137) in form of a stout claw, terminal claw with patch of spinules and setae; patch of spinules present also on penultimate segment. Furca (figs. 138 and 139) usually spatulate but sometimes rounded at tips of spines (fig. 139). Accessory processes present on either side of furca and vary in length. Pillai (1961, p. 114) noted differences in development of these processes. Figures 138 and 139 show two extremes in development within the sample studied here—both from *Tylosurus acus acus* in the western Atlantic. Intermediate forms were common.

Legs 1 to 3 biramose. Leg 1 (fig. 140) exopod 2-segmented, first segment without spines and setae, second segment with three terminal spines and three inner setae; endopod 1-segmented, small, bearing two small terminal spines. Leg 2 (fig. 144) exopod 3-segmented, first two segments each with one inner seta and one small spine on outer distal corner, last segment bearing six setae and two spines; endopod 3-segmented, first segment with an inner seta, second segment with two inner setae and a spine on outer distal corner, terminal segment bearing five setae. Leg 3 (fig. 142) exopod 2-segmented, basal segment with prominent claw on outer distal corner, terminal segment bearing eight short setae; endopod 2-segmented, basal segment with one inner seta, terminal segment with four terminal setae. Leg 4 (fig. 143) uniramose; exopod with three segments, basal two segments each with short spine on outer distal corner, terminal segment with one long and two short spines. Leg 5 represented by one long process on each posterior corner of genital segment. Leg 6 absent. Egg strings uniseriate.

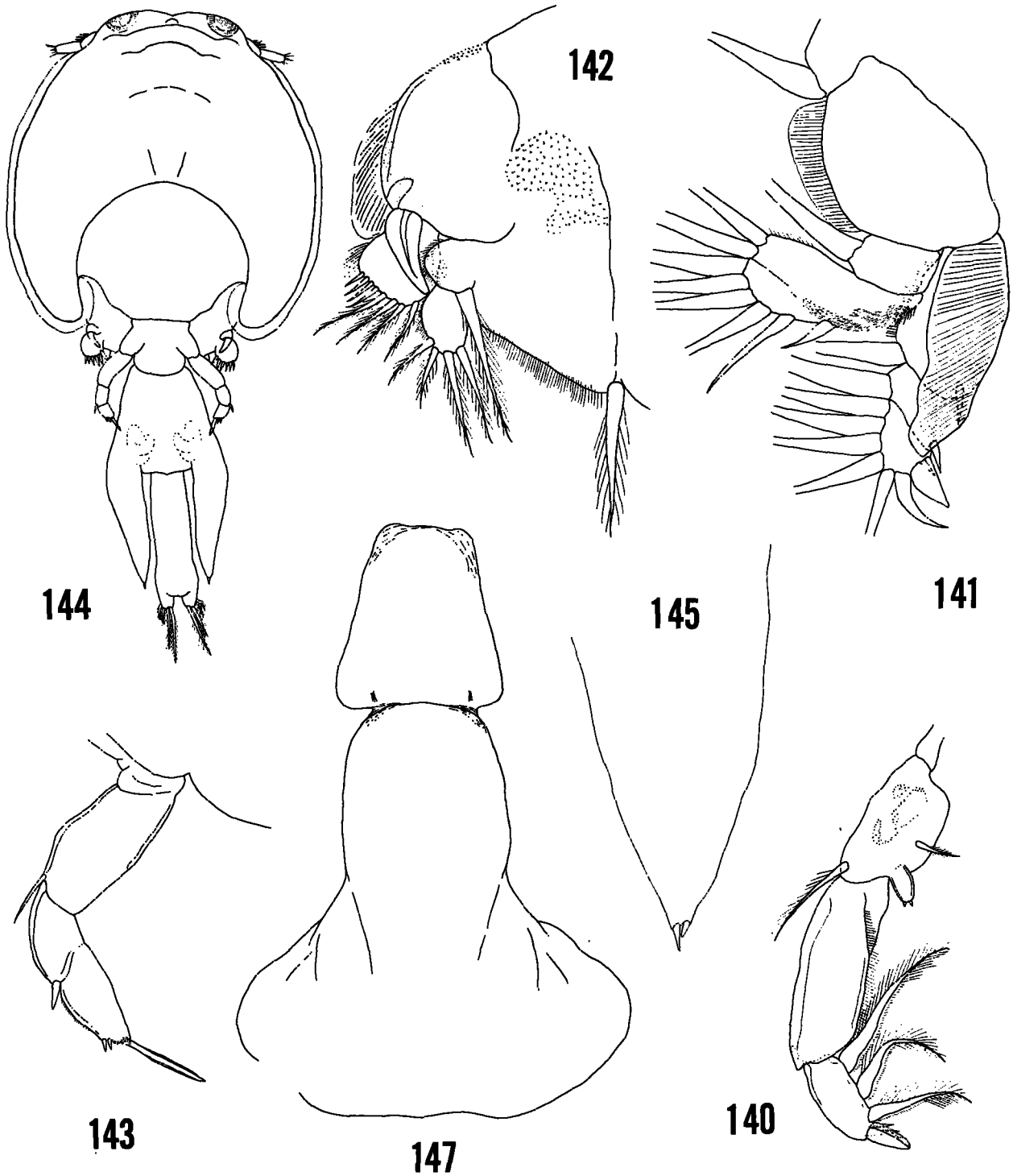
Immature female.—Body form as in figure 144. Total length 1.8 mm. Greatest width 0.82 mm. Appendages as in adult except for two spines at tip of leg 5 (fig. 145). The two immature forms are from *Tylosurus a. acus* from Honduras and *T. crocodilus* from Thailand.

Remarks.—The large sample of *C. laciniatus* studied here permits observations on size variation. Pillai (1961, p. 114) noted differences in lengths of adult females depending on host. On the basis of his collections from Indian Ocean needlefishes, he stated that those specimens from *Ablennes hians* were distinctly larger (9.8 mm.) than those from *Tylosurus crocodilus* (5.0 mm.). Kirtisinghe (1937, p. 441) noted that his specimens of this copepod from *Strongylura leiura* were larger (7.5 mm.) than those from *S. strongylura* (5.0 mm.). Nuñes-Ruivo (1962b) compared the relative lengths of four body divisions of seven females from a single *Ablennes hians* from Angola.

From the sample reported on here, 69 ovigerous females from 65 collections representing six host species were measured. Total lengths were measured from the anteriormost point on the cephalon to the end of the 5th legs. In most specimens the 5th legs extend slightly beyond the caudal rami. On the basis of these measurements, it is apparent



FIGURES 131–139.—*Caligus* and *Caligodes*. 131–132. *Caligus* species D, female (continued). 131. Endopod of second leg. 132. Fourth leg. 133–139. *Caligodes laciniatus* (Krøyer), female. 133. Caudal ramus, ventral view. 134. First antenna. 135. Second antenna. 136. Oral area. 137. Maxilliped. 138. Area of sternal furca. 139. Area of sternal furca.



FIGURES 140–145.—*Caligodes laciniatus* (Krøyer), female (continued). 140. First leg. 141. Second leg. 142. Third leg. 143. Fourth leg. 144. Dorsal view, immature female. 145. Fifth leg, immature female. 147. *Lernanthropus belones* Krøyer, female, dorsal view.

that size depends on the host (table 2). In addition to total length, we determined the proportional lengths of four main body divisions (cephalon, thorax, genital segment, and abdomen). The size of the cephalon varied the least from one host to another. The total length of the copepod was nearly seven times the length of the cephalon in specimens from *A. hians*, whereas in those from *T. crocodilus* the ratio was only 4.5:1. From other hosts the ratio was intermediate as follows: *T. acus*, 5.1:1; *Lhotskia gavialoides*, 5.3:1; and *S. leiura*, 5.9:1. These ratios suggest that the part of the copepod most affected by the host is the more posterior. Considering the habitat of this species (generally beneath the oral valve), the copepod may have to grow to lengths which permit anal respiration and elimination by extending that portion of the body beyond the edge of the oral valve, and permit egg strings to be exposed for proper oxygenation and larval escape. Figure 146 shows three specimens in place under the lower jaw oral valve of *Ablennes hians*.

TABLE 2.—*Total lengths of ovigerous female* Caligodes laciniatus, *by hosts and by areas*

Host and, in parentheses, its maximum body length (mm.)	Copepod total length			
	Atlantic	Indo-West Pacific	Eastern Pacific	Average length, by host
	Mm.	*Mm.*	*Mm.*	*Mm.*
Ablennes hians (725)	5.3 6.2	----------	5.3	
	5.3 6.8	----------	5.6	6.03
	5.4 6.9	----------	6.6	
	5.9 7.1	----------	----------	
Lhotskia gavialoides (665)	----------	3.9	----------	
	----------	4.5	----------	4.66
	----------	5.6	----------	
Strongylura leiura (501)	----------	4.1	----------	
	----------	4.2	----------	
	----------	4.3	----------	4.54
	----------	4.8	----------	
	----------	5.3	----------	
Tylosurus acus (950)	2.4 3.6	3.2	3.7	
	3.0 3.8	3.7	4.7	
	3.1 3.9	4.5	----------	
	3.2 4.1	----------	----------	3.77
	3.2 4.4	----------	----------	
	3.3 4.5	----------	----------	
	3.4 4.7	----------	----------	
	3.4 5.4	----------	----------	
Tylosurus crocodilus (860)	3.1 -----	2.3 3.2	3.4 3.8	
	3.4 -----	2.5 3.2	3.5 3.8	
	3.9 -----	2.6 3.4	3.6 3.8	
	4.3 -----	2.7 3.4	3.8 4.7	3.47
	4.4 -----	2.8 3.8	3.8 -----	
	----------	3.0 4.0	----------	
	----------	3.1 4.3	----------	
Tylosurus choram (415)	----------	2.9	----------	2.90
Average length, by area	4.36	3.70	4.29	

Geography does not seem to influence total length of the copepod except as it determines the distribution of the hosts (see table 2).

In a paper on the genus *Gloiopotes*, Cressey (1967) noted that the average size of the adult female *G. watsoni* depended on the host. Whether size differences are influenced primarily by the host or secondarily by the environment of the host cannot be determined at present, but the fact that the host influences the morphometrics of parasitic copepods is becoming more apparent. It is also obvious that the absolute size of parasitic copepods cannot be considered a reliable taxonomic character.

FAMILY ANTHOSOMATIDAE

Two species of *Lernanthropus* were collected. We have determined that only two species, *L. tylosuri* and *L. belones*, are found on needlefishes. Others described from needlefishes have been synonymized with these two.

Lernanthropus belones Krøyer

Figures 147 to 156, Plate 3 (a–c)

Lernanthropus chlamydotes Wilson, 1922, p. 48.

Specimens studied.—A total of 689 specimens, including both sexes, from 80 collections from 11 host species. A detailed list of these collections is provided below: *Ablennes hians*, Puerto Rico; *Platybelone argalus*, Bermuda (2 collections); *Strongylura anastomella*, Suruga Bay, Japan; *Strongylura exilis*, San Diego, Calif. (3 collections); Baja California (2 collections); Panama (Pacific); *Strongylura incisa*, Ebon Island, Marshall Islands (2 collections); Arnhem Land, Australia; Philippines (2 collections); Singapore (2 collections); Gilbert Islands; *Strongylura marina*, Beaufort, N.C.; Morehead City, N.C.; St. Simons Island, Ga. (3 collections); Florida, west coast (3 collections); Florida, east coast (2 collections); Venezuela; Trinidad; *Strongylura notata*, Florida, west coast (7 collections); Florida, east coast (3 collections); Andros Island, Bimini Island, Bahamas; Yucatan; Cuba (2 collections); Jamaica; *Strongylura scapularis*, Balboa, Canal Zone (2 collections); Guayaquil, Ecuador (2 collections); *Strongylura strongylura*, Bombay, India; Madras, India; Singapore; China; Philippines; *Strongylura timucu*, Florida, west coast (5 collections); Florida, east coast (3 collections); Bahamas (2 collections); Cuba; Jamaica (3 collections); Puerto Rico (4 collections); Virgin Islands (2 collections); Colon, Panama; Yucatan (2

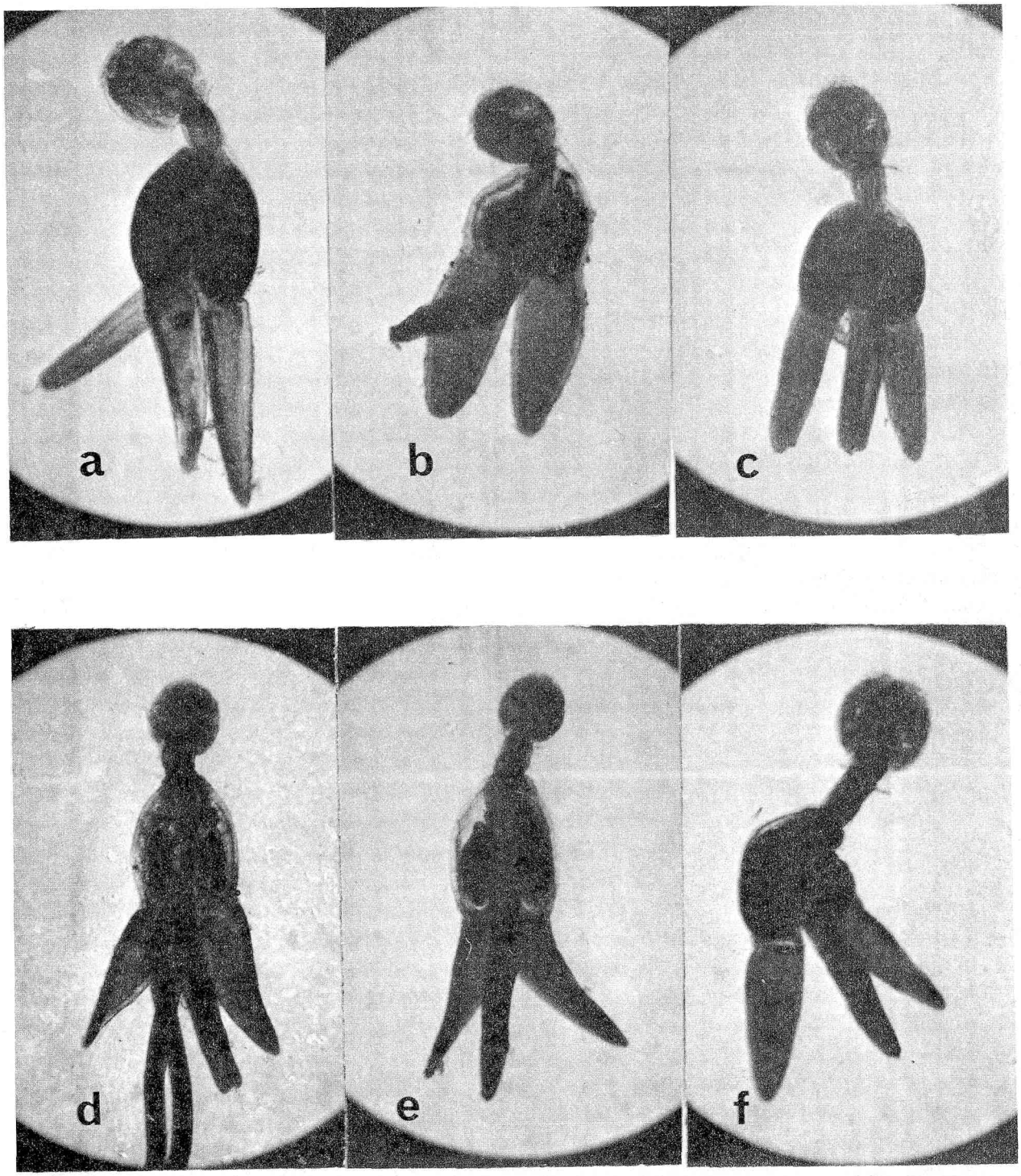


PLATE 2.—*Caligodes laciniatus* (Krøyer), female. a. From *Tylosurus acus* (Western Atlantic). b. From *Tylosurus acus* (Gulf of Mexico). c. From *Tylosurus acus* (Revillagigedo Islands). d. From *Ablennes hians* (Surinam). e. From *Ablennes hians* (Gulf of Guinea). f. From *Tylosurus crocodilus* (Jamaica).

collections); Honduras; Brazil (2 collections); *Tylosurus punctulatus*, Sandakan, Borneo.

Female.—Body form as in figure 147. Average total length 2.58 mm., based on 128 ovigerous females from six host species. Specimens from Pacific waters average larger (4.02 mm.) than those from the Atlantic (2.22 mm.). Most of our collections were from the Atlantic; if more material were available from the Pacific the average total length for all collections would be greater. The total length (in millimeters) of each adult female in 36 collections from six host species is presented below. Note that the variation between collections is greater than the variation within a collection.

Strongylura notata	2.19 (average).
Sarasota, Fla.	1.7, 1.8, 1.9, 1.9, 1.95.
Sarasota, Fla.	1.95, 2.0.
Sarasota, Fla.	3.0, 3.15, 3.15, 3.2, 3.3, 3.4.
Sarasota, Fla.	2.8, 2.8, 3.0, 3.0, 3.15.
Key Biscayne, Fla.	1.95, 2.0, 2.1.
Andros Island, Bahamas	1.65, 1.7.
Cuba	2.3, 2.4, 2.5, 2.6.
Yucatan	1.7, 1.95, 2.5.
Strongylura timucu	2.10 (average).
Sanibel Island, Fla.	1.5.
Sarasota, Fla.	1.7, 1.8, 1.9, 1.9, 1.9, 1.9, 2.0.
Cedar Keys, Fla.	1.6, 1.7, 1.7, 1.8, 2.1.
Key Biscayne, Fla.	2.2.
Key Biscayne, Fla.	1.95, 2.1, 2.1, 2.2.
Bahamas	2.0, 2.1, 2.2.
Bahamas	2.0, 2.3.
Yucatan	2.1, 2.25, 2.4, 2.4, 2.5.
Yucatan	2.1, 2.2, 2.3, 2.4, 2.7.
Puerto Rico	1.9, 2.2, 2.2.
Puerto Rico	2.2, 2.2, 2.25, 2.3.
Virgin Islands	1.9, 1.95, 2.2.
Colon, Panama	2.0.
Brazil	2.4, 2.5, 2.5.
Strongylura marina	2.44 (average).
Beaufort, N.C.	2.1, 2.3, 2.3, 2.3, 2.3, 2.5.
Beaufort, N.C.	2.9, 3.1, 3.3, 3.4, 3.4.
Beaufort, N.C.	2.6, 2.7, 2.8, 2.85, 2.9, 3.0.
Jekyll Island, Ga.	1.9, 1.9, 2.25, 2.4, 2.5.
Flagler Beach, Fla.	1.8, 2.0.
Amelia River, Fla.	1.65, 1.9, 1.9, 1.95.
Strongylura incisa	3.93 (average).
Marshall Islands	4.0, 4.2, 4.2, 4.4, 4.5.
Gilbert Islands	4.2.
Philippines	3.15.
Arnhem Land, Australia	2.8.
Strongylura exilis	4.08 (average).
San Diego, Calif.	2.5, 2.7.
San Diego, Calif.	3.6, 3.7, 3.75, 3.9, 4.5.
San Diego, Calif.	4.4, 4.5, 4.7, 4.9, 4.9, 4.95.
Strongylura scapularis	3.20 (average).
Balboa, Canal Zone	3.2, 3.2.

The mean total length clearly varies with the host or geographic area or both. Atlantic *L. belones* are generally shorter than those from the Pacific. The lengths are not always consistent within a geographic area, however. For example, the lengths of the copepods from four collections from *S. notata* from Sarasota, Fla., vary considerably from collection to collection; each collection was made in July–August but in different years (1965–68). Another example is the three collections from *S. exilis* from San Diego, Calif.

Cephalon about one-third total body length. Posterior corners without horns (fig. 147). No further description of the female is given here as the appendages are identical to those described for *L. cornutus* (=*L. tylosuri*) by Shiino (1965). Shiino stated that the armature of the second pair of legs differs in the two species but we could not find this difference in the collections of both species reported herein.

Male.—Body form as in figure 148 and plate 3. Total length of six specimens averages 1.53 mm. (1.10–2.18 mm.). Specimens from Pacific areas are larger (1.42, 1.42, 1.80, and 2.18 mm.) than those from the Atlantic (1.10 and 1.27 mm.). Cephalon slightly wider than long and composing about one-quarter total body length.

Second antenna (fig. 149) a simple claw, surface of segments covered with small pits. Mandible

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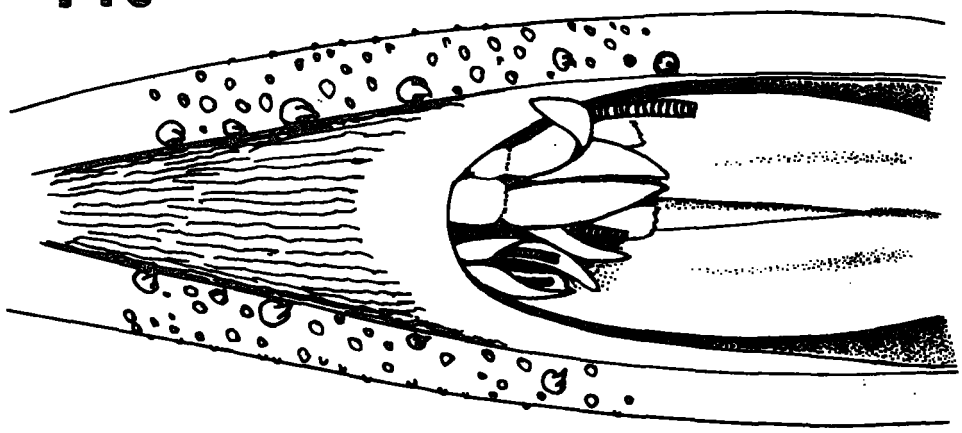


FIGURE 146.—Lower jaw of *Ablennes hians* showing three female *Caligodes lacintatus* attached beneath oral valve.

(fig. 150) of usual caligoid type with about six teeth. First maxilla (fig. 150) with inner posteriorly directed process near mouthtube and outer lobe bearing three setae. Second maxilla (fig. 151) with stout basal segment, distal two segments in form of a claw; tip of maxilla with rows of spinules (fig. 152).

Leg 1 (fig. 153) exopod 1-segmented with five broad distal spines, row of spinules near base of innermost spine; endopod 1-segmented bearing a single long seta and spinules scattered over distal half. Leg 2 (fig. 154) exopod 1-segmented with distal border bearing rows of spinules, posterior surface of segment with median ridge bearing spinules. Leg 3 in form of an elongate lateral process tipped by an area bearing several (6–10) short spines, spinose area sometimes knoblike. Leg 4 in form of an elongate process with bifurcated tip (figs. 155, 156), each arm of bifurcation bearing short spines at tip; as in leg 3 spinose area often knoblike, area between rami with shallow indentation.

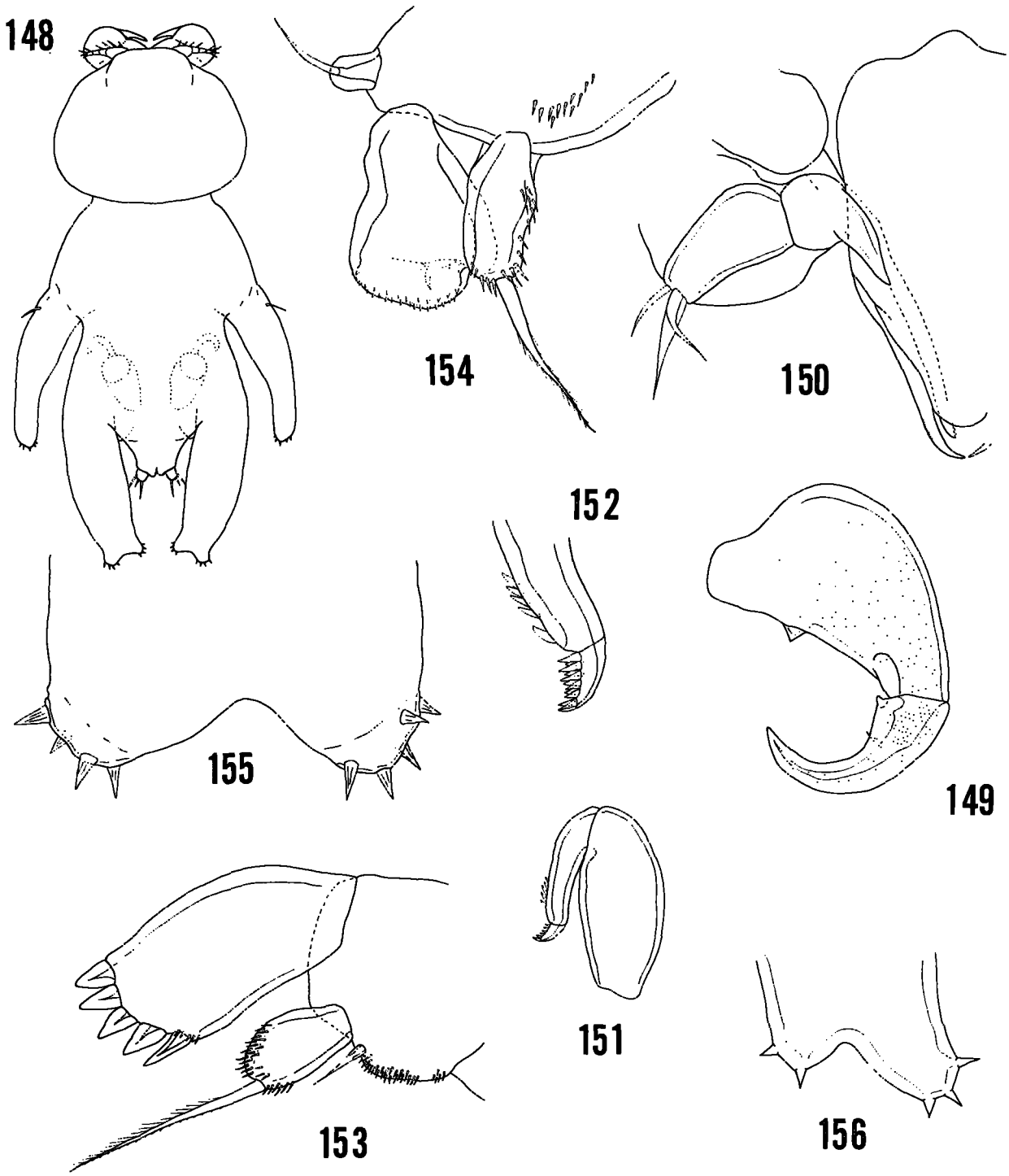
Remarks.—This species is closely related to *L. tylosuri* (= *cornutus*) also commonly found on needlefishes. A discussion of the characters used to separate these two species and of the host specificity of each follows the description of *L. tylosuri*.

***Lernanthropus tylosuri* Richiardi**

Figures 157 to 162, Plates 3(d-f), 4

Lernanthropus cornutus Kirtisinghe, 1937, p. 448.

Specimens studied.—A total of 474 specimens from 99 collections, including both sexes, from 14 host species. A detailed list of these collections is provided below: *Ablennes hians*, Woods Hole, Mass.; off Virginia coast; Haiti; Recife, Brazil; Gulf of Guinea (3 collections); Sierra Leone (3 collections); Mauritius; Philippines (2 collections); Japan (10 collections); Formosa; Marshall Islands; Hawaii; Gulf of California; Acapulco, Mexico; Panama (Pacific); Cabo Blanco, Peru; *Platybelone argalus*, Fernando Póo, Gulf of Guinea; *Strongylura leiura*, Persian Gulf; Philippines (2 collections); *Strongylura exilis*, Baja California; northern Peru; *Strongylura incisa*, Queensland, Australia; *Strongylura marina*, British Honduras; *Strongylura strongylura*, Malay Peninsula (2 collections); *Strongylura timucu*, Rio de Janeiro, Brazil; *Strongylura urvillii*, Philippine Islands; *Strongylura anastomella*, Japan (9 collections); Korea (2 collections); *Tylosurus acus*, Puerto Rico; Virgin Islands; Honduras; Sierra Leone; Angola (3 collections); Java; Philippines (2 collections); Revillagigedos Island, Mexico; Gulf of California; Acapulco, Mexico; Panama (Pacific); *Tylosurus choram*, Red Sea; *Tylosurus crocodilus*, Matecumbe Key, Fla.; U.S. east coast; Bahamas (3 collections); Venezuela (5 collections); Red Sea; Kenya; Zanzibar; Nosy Bé, Madagascar (3 collections); Mauritius; Seychelles; Gulf of Aden; Persian Gulf; Arabian Gulf; Ceylon; Kerala, India; Java; Singapore; Gulf of Thailand; North Borneo (3 collections); Philippines (3 collections); Japan; Marshall



FIGURES 148–156.—*Lernanthropus belones* Krøyer, male. 148. Dorsal view. 149. Second antenna. 150. Oral area. 151. Second maxilla. 152. Tip of second maxilla. 153. First leg. 154. Second leg. 155. Fourth leg. 156. Fourth leg.

Islands; Hawaii (2 collections); Matzatlan, Mexico; Panama (Pacific); *Tylosurus punctulatus*, Philippines (2 collections).

Female.—Body form as in plate 4 and figure 157. The female of this species was redescribed by Shiino (as *L. cornutus*) in 1965 so no further description is given here except as pertains to variation in the lateral cephalic processes. These processes, by which the females of this species can be separated from the preceding species, show great variation in development. However, little correlation could be found with host or locality regarding this variation. Plate 4 illustrates several examples of variation in this character. In a series of 52 specimens from as many collections the width of the cephalon across the lateral processes was compared with the length of the cephalon. Unlike *L. belones*, where the width of the cephalon at the posterior corners is less than or occasionally equal to the cephalon length, the width of the cephalon of *L. tylosuri* at this point, because of these processes, is significantly greater than the cephalon length. A summary of the measurements for the 52 collections is presented below.

The average widths, expressed as percentage of cephalon length to width, for four host species are as follows:

A. hians	66.7 (13 collections)
S. anastomella	76.5 (7 collections)
T. crocodilus	77.3 (28 collections)
T. acus	75.9 (9 collections)

The average widths, expressed as percentage of cephalon length to width, by geographical area are as follows:

Western Atlantic	73.4 (13 collections)
Eastern Atlantic	73.0 (6 collections)
Indian Ocean	79.4 (9 collections)
Central and western Pacific	74.5 (23 collections)
Eastern Pacific	77.3 (6 collections)

Male.—Body form as in figure 158 and plate 3. Total length 2.4 mm. (single specimen from *S. anastomella*—Japan). Cephalon wider than long (0.82 by 0.68 mm.) and making up about one-quarter of the body length. Caudal rami armed with four setae as indicated in figure 159. Appendages as in *L. belones* except for the following subtle differences. Tip of leg 3 (fig. 160) with the spine-bearing portion knoblike. End of leg 4 (figs. 161, 162) bifurcate (as in *L. belones*), each branch with knoblike tip bearing short spines; indentation between branches deeper than in *L. belones* (compare figs. 155 and 156 with 160 and 161).

Remarks.—*L. tylosuri* and *L. belones* are common on needlefishes. In the 146 collections of these species the two species of copepods were never found on the same host individual. The following list shows the frequency of each copepod species on each host species and demonstrates host specificity within each species of copepod (the numbers refer to numbers of collections):

	L. tylosuri	*L. belones*
Ablennes hians	12	1
Platybelone argalus	1	1
Strongylura exilis	0	4
S. incisa	1	7
S. leiura	3	0
S. marina	1	12
S. notata	0	15
S. scapularis	0	4
S. strongylura	2	4
S. urvillii	1	0
S. timucu	0	26
S. anastomella	9	0
Tylosurus acus	10	0
T. crocodilus	31	0
T. punctulatus	2	0

L. tylosuri clearly is common on *Ablennes hians*, *Strongylura leiura*, *S. anastomella*, and the species of *Tylosurus*, whereas *L. belones* is predominant on the other species of *Strongylura*.

FAMILY LERNAEIDAE

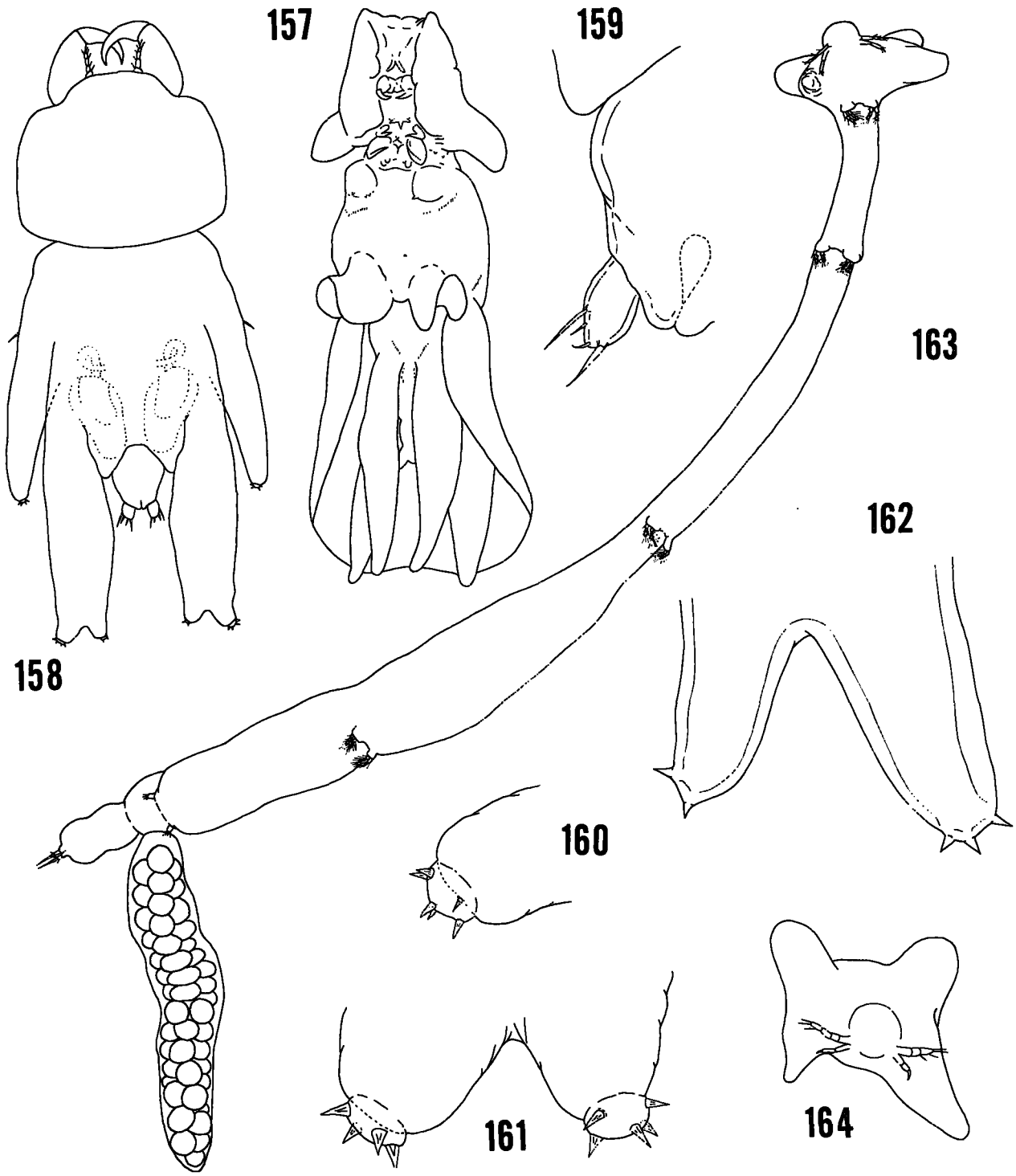
Two members of this family were collected, *Lernaea* sp. and *Lernaeenicus* sp. Neither of these is considered a specific parasite of needlefishes.

Lernaea Sp.

Figures 163, 164

A single ovigerous female (6.9 mm. long) was removed from the pit immediately behind the left pectoral fin of a *Xenentodon cancila* collected in an unknown fresh-water locality in southeast Asia.

The copepod may be an undescribed species but in view of the amount of variation which occurs within the species of this genus (see Ho, 1961) and the lack of locality data, description on the basis of a single specimen would be premature. Figures of the whole animal (fig. 163) and the anchoring apparatus (fig. 164) are provided. One of the horns seems to be deformed in this specimen.



FIGURES 157–164.—*Lernanthropus tylosuri* Richiardi and *Lernaca* species. 157–162. *L. tylosuri* female. 157. Ventral view, after Shiino. Same, male. 158. Dorsal view. 159. Caudal ramus, ventral view. 160. Third leg. 161. Fourth leg. 162. Fourth leg. 163–164. *Lernaea* species, female. 163. Ventral view. 164. Anterior end of body.

The spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1.....	I:1	0:1	I:1	0:1	I:1	0:1	I:1	0:1
Seg. 2.....	I:1	0:1	I:1	0:2	I:1	0:2	I:1	0:2
Seg. 3.....	II:5	II:4	III:5	II:4	III:5	II:4	III:5	II:3

On the basis of the shape of the anchor, the specimen seems to be closely related to *Lernaea composita* Wilson, 1924 described from the electric catfish, *Malapterus electricus*, in Egypt.

***Lernaeenicus* Sp.**

Specimens studied.—A single female embedded at the base of the pectoral fin of a specimen of *Tylosurus crocodilus* from Manila, Philippines.

FAMILY LERNAEOCERIDAE

***Lernaeolophus sultanus* (Milne-Edwards)**

Specimens studied.—One collection containing one immature female from the tongue of *Platybelone argalus trachura* taken at Ascension Island; one collection containing two females from the roof of the mouth of *Strongylura marina* collected off Belize, British Honduras; and one collection of two females from the roof of the mouth of *Tylosurus a. acus* from Haiti.

Remarks.—This copepod has been considered recently by Kabata (1968) so no further description is added here. His investigations showed this species to be a lernaeocerid and not a pennellid as thought by Yamaguti (1963). *L. sultanus* is not common on needlefishes, and they are probably not its preferred host. It has been previously reported from *Acanthocybium solandri*, *Caranx ascensionis*, *Istiophorus gladius*, *Haemulon plumieri*, *Maena vulgaris*, and two species of *Serranus*.

Order Philichthyidea

A single species of the family Philichthyidae was collected—a new species of *Colobomatus* from the cephalic canals of needlefishes.

FAMILY PHILICHTHYIDAE

***Colobomatus goodingi* Cressey and Collette, New Species**

Figures 165 to 174

Specimens studied.—Sixty-five collections from 7 host species containing 190 females as listed below: *Ablennes hians*, Cuba; Haiti; Sierra Leone (2 collections); Dahomey; Gabon; Torres Strait, Australia (2 collections); Acapulco, Mexico; Panama (Pacific); *Strongylura notata*, Sanibel Island, Fla.; Sarasota, Fla. (2 collections); Tampa Bay, Fla.; Alligator Harbor, Fla.; Key Biscayne, Fla. (3 collections); Bimini, Bahamas (2 collections); Providence Island, Caribbean Sea; *Strongylura marina*, west coast of Florida; Everglades Park, Fla.; Clearwater, Fla.; Alligator Harbor, Fla.; Panama City, Fla.; *Strongylura timucu*, west coast of Florida (2 collections); Haiti (2 collections); Puerto Rico (2 collections); Virgin Islands; Curaçao; *Strongylura exilis*, Panama (Pacific); *Tylosurus acus*, Gulf of Mexico (2 collections); Bahamas (2 collections); Angola (2 collections); Philippines; Acapulco, Mexico; Panama (Pacific); Cabo Blanco, Peru; *Tylosurus crocodilus*, Virginia Key, Fla.; Bahamas; Trinidad; Venezuela; Cameroons; Red Sea; Gulf of Aden; Madagascar (4 collections); Madras, India; Kerala, India; Ceylon; Java; Manila, Philippines; Marianas Islands; Solomon Islands; Marshall Islands; Panama (Pacific) (2 collections); Cocos Island (Eastern Pacific).

Holotype female (USNM 125700) and five paratype females (USNM 125701) from *Strongylura notata* from Bimini.

Female.—Body form as in figure 165. Total length based on an average of 28 ovigerous females from the four host species 4.4 mm. (2.7–7.1 mm.). Greatest width 1.9 mm. (0.82–2.78 mm.).

Cephalon with single lobe projecting anterior to first antenna (in all other species except *C. muraenae* this lobe is double). Three thoracic segments partially separated from each other posterior to cephalon, each segment only slightly wider than cephalon. Next following segment greatly expanded, each side bearing an anteriorly and posteriorly directed lobe; this segment composes about one-third total body length. The following segment with a lateral, well-developed lobe on each side. Three remaining segments (abdomen?) of about equal width and incompletely divided from each other, last segment with a posteriorly directed lobe projecting between caudal rami giving posterior portion of body a triramose appearance.

First antenna apparently 4-segmented, each segment bearing a few long setae; the total length of this appendage is only 26.5 μ. Because of its small

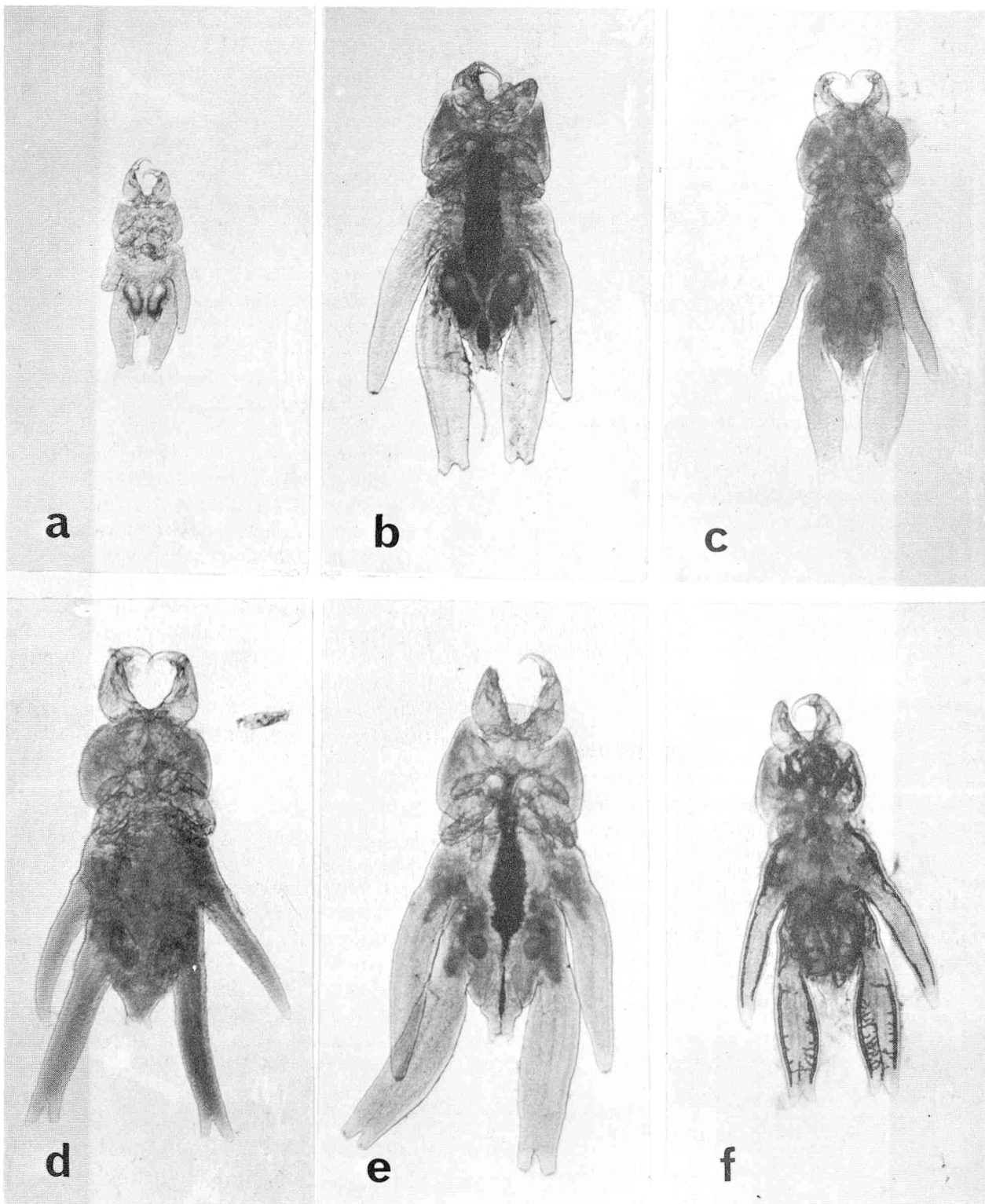


PLATE 3.—*Lernanthropus belones* Krøyer, male. a. From *Strongylura strongylura* (Bombay, India). b. From *Ablennes hians* (Puerto Rico). c. From *Strongylura exilis* (San Diego), *Lernanthropus tylosuri* Richiardi, male. d. From *Strongylura anastomella* (Japan). e. From *Ablennes hians* (Marshall Islands). f. From *Ablennes hians* (Philippines).

size it was not possible even with the highest magnification to see enough details to make an accurate drawing of this appendage (five specimens examined).

Remaining appendages consisting of mandible (fig. 166), first maxilla (fig. 167), and second maxilla (fig. 168) contained within the mouthtube. Figure 169 illustrates position of appendages within tube. All other appendages lacking. Egg sacs broken on all but one specimen; sacs held close to body on either side of abdomen (represented by dotted lines on fig. 165) and containing 50 to 75 eggs.

Color in life, cream.

Male.—Unknown.

Etymology.—This species is named for Richard Gooding who made preliminary examinations of this species and first recognized it as new.

Remarks.—This species can be separated from all other species of *Colobomatus* except *C. muraenae* by the two cephalic lobes present in the other species. It can be separated from *C. muraenae* by the presence of a posterior lobe between the caudal rami in the new species (no such lobe in *C. muraenae*).

Sites of infestation.—*Colobomatus goodingi* has been found in three of the major lateral line canals on the heads of needlefishes: preoperculomandibular (from the tip of the lower jaw posteriorly); interorbital (above each eye); and preorbital (short canal in front of eye). *C. goodingi* has occasionally been found on the upper jaw which does not appear to have a distinct branch of the lateral line system. The most common site of infestation (51 of 66) in *Strongylura notata* is the lower jaw, where a large easily visible swelling forms (fig. 171). The next most common site in *S. notata* is in the interorbital canal (11 of 66 sites). Only three infestation sites were on the upper jaw and one was in the preorbital canal. Similar swellings were present in infested *S. marina* and *S. timucu*.

No distinct capsule (fig. 171) such as is present in western Atlantic species of *Strongylura* was found in any specimens of *Tylosurus* or *Ablennes*. In *Ablennes*, expansion of the lateral line canal is usually internal and makes it very difficult to detect infested specimens; consequently, *C. goodingi* was at first thought to be confined to western Atlantic species of *Strongylura*.

Twenty-one of 24 Venezuelan specimens of *Tylosurus crocodilus* (132–300 mm. BL) were infested with *C. goodingi*. Of 46 sites, 37 were on the lower jaw (19 on the left and 18 on the right) and 9 were in the interorbital canal (4 on the left and 5 on the right). Three Bahamian and one Jamaican specimens each had an infestation site on the right side of the lower jaw. A specimen of *T. crocodilus* from Haiti had one small *C. goodingi* in the left interorbital canal and one on each side of the lower jaw.

Histopathology.—Seven *Colobomatus* lesions were examined in step-serial sections prepared from mandibles and maxillae of four *Strongylura notata* from Bimini. These tissues had been fixed in 4 percent formalin and were decalcified in 5 percent formic-citrate before sectioning. Staining was hematoxyline and eosin.

Reactions to the *Colobomatus* were variable, ranging from almost none (fig. 172) to a nearly complete obliteration of the involved lateral line canal by granulation tissue, inflammatory infiltrate, and, in some infestations, new bone formation (fig. 173). New bone formation was always orderly and showed no evidence of neoplastic transformation. In one example the formation could be related to fracture of an adjacent bone trabeculum. New bone formation was always associated with marked chronic osteitis or osteitis combined with microfracture.

The epithelium lining the canals occupied by *Colobomatus* was generally only a few cells thick, and the cells were extremely flat except where underlying inflammation was pronounced. In the latter situation, the epithelium was thickened and usually diffusely infiltrated by the cellular reaction.

The inflammatory infiltrates were composed mainly of lymphocytes and macrophages. Mononuclear eosinophils were moderately numerous, often forming small clusters. Occasionally, the granulation tissue contained fairly discrete granulomas, and the epithelioid cells within these granulomas contained deposits of eosinophilic material, possibly derived from phagocytosis of the necrotic ova commonly present within the cavity (fig. 174).

HOST-PARASITE LIST

The species of copepods collected from each species of needlefish are given in this section. The

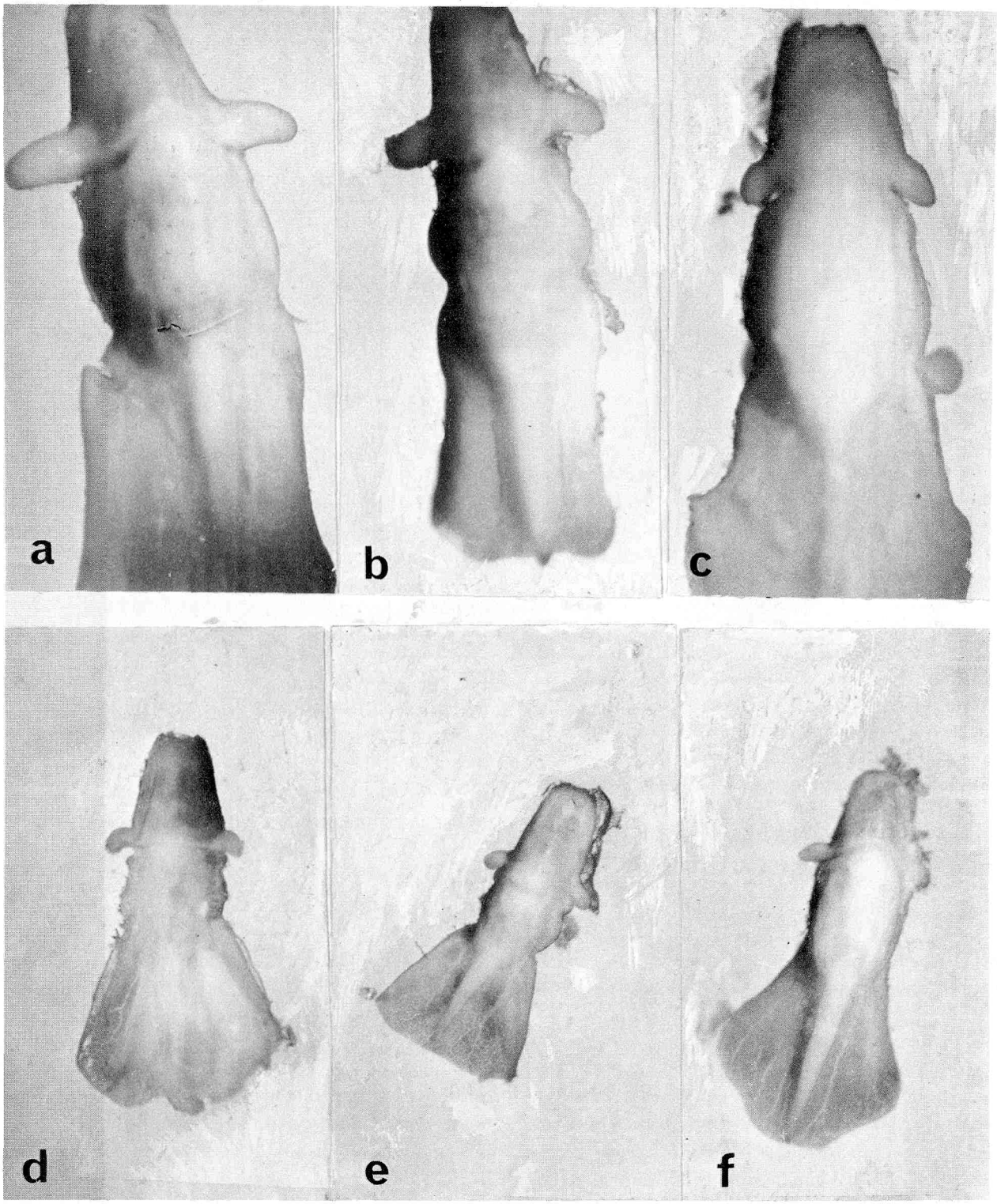
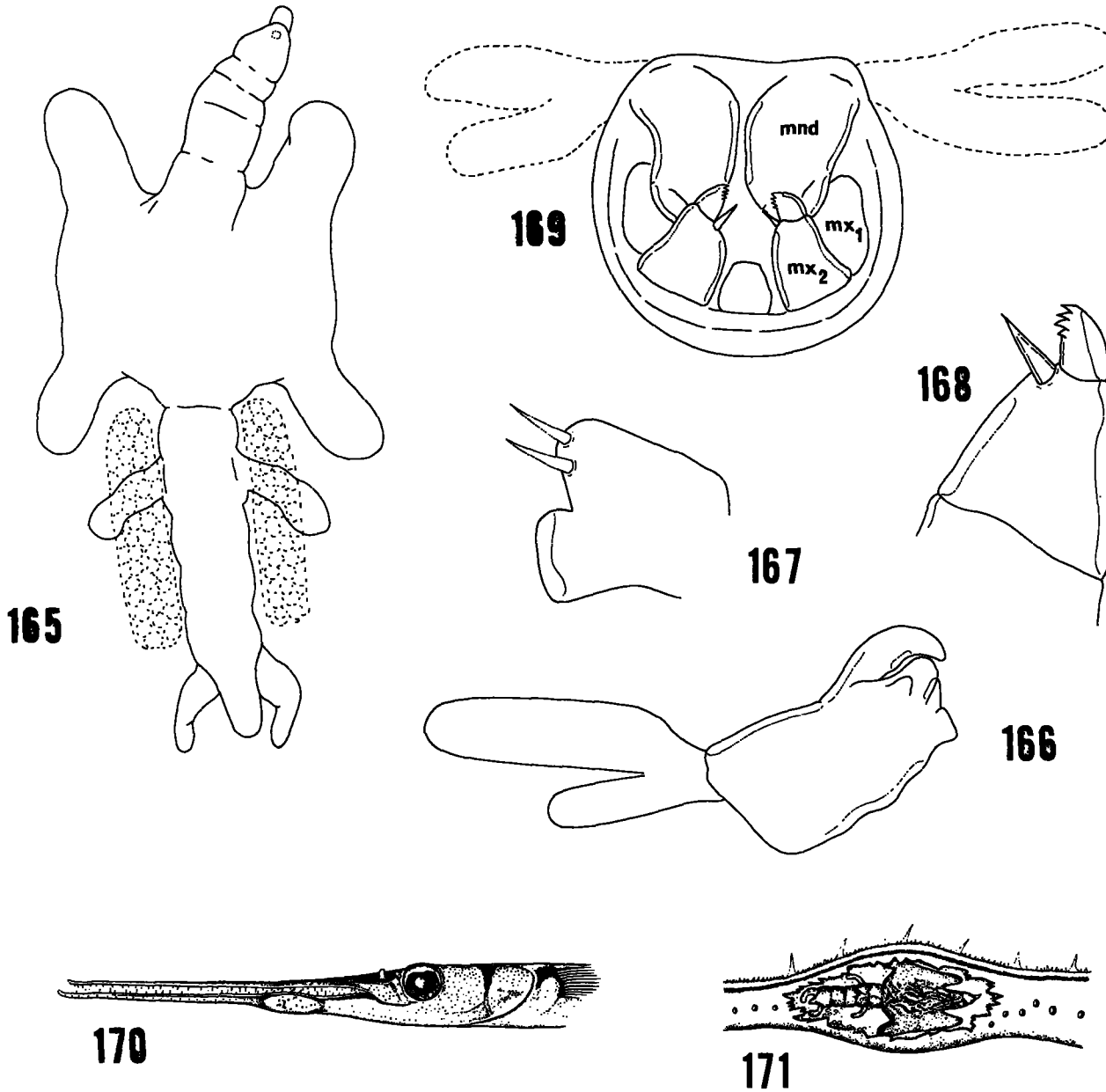


PLATE 4.—*Lernanthropus tylosuri* Richiardi, female. a. From *Ablennes hians* (Marshall Islands). b. From *Ablennes hians* (Gulf of Guinea). c. From *Strongylura anastomella* (Japan). d. From *Tylosurus acus* (Virgin Islands). e. From *Tylosurus crocodilus* (Venezuela). f. From *Tylosurus crocodilus* (Madagascar).



FIGURES 165–171.—*Colobomatus goodingi*, new species, female. 165. Dorsal view. 166. Mandible. 167. First maxilla. 168. Second maxilla. 169. Oral area. 170. Lateral view of head of *Strongylura notata* showing site of *Colobomatus* infestation on lower jaw. 171. *Colobomatus* site on lower jaw of *Strongylura notata* with covering of capsule removed.

needlefish species are listed alphabetically; the four worldwide species are further listed regionally, from the western Atlantic to the eastern Pacific. Total numbers of hosts examined, size range (in millimeters BL, body length, and SL, standard length, where possible), and brief description of host range are also included. The copepod lists include total numbers, sex, and general localities. Literature records are given following our material.

Ablennes hians (Valenciennes)

A large (maximum size 725 mm. BL) offshore marine needlefish found worldwide in tropical and subtropical seas (see fig. 175).

WESTERN ATLANTIC

81 specimens (83–630 mm. BL) from 30 collections.

Caligodes laciniatus, eight females from six specimens (200–240 mm. BL). Florida; Mississippi; Caribbean Sea; Surinam; Brazil.

Parabomolochus bellones, 12 males and 96 females from 31 specimens (169–535 mm. BL). Woods Hole, Mass.; Virginia; Florida; Mississippi; Grand Bahamas; Haiti; Caribbean Sea; Honduras; Recife, Brazil.

Lernanthropus tylosuri, six females and three males from four specimens (353–455 mm. BL). Woods Hole, Mass.; New Point, Va.; Port-au-Prince, Haiti; Recife, Brazil.

Lernanthropus belones, three males and one female from one specimen (459 mm. BL). Western Puerto Rico.

Colobomatus goodingi, two females from interorbital canals of two specimens (455–630 mm. BL). Cuba; Port-au-Prince, Haiti.

EASTERN ATLANTIC

37 specimens (132–530 mm. BL) from 17 collections.

Caligodes laciniatus, 58 females from nine specimens (207–530 mm. BL). Cape Verde Islands; Guinea; Sierra Leone; Ghana; Gabon; Angola.

Parabomolochus bellones, 1 male and 26 females from 17 specimens (132–530 mm. BL). Guinea; Sierra Leone; Ghana; Dahomey; Gabon.

Lernanthropus tylosuri, five females and one male from four specimens (418–530 mm. BL). Sierra Leone; Gabon.

Colobomatus goodingi, 15 females from 15 specimens (147–530 mm. BL). Sierra Leone; Dahomey; Gabon.

Caligus sp. A, two males and six females from four specimens (418–530 mm. BL). Sierra Leone; Gabon.

INDIAN OCEAN

31 specimens (84–725 mm. BL) from 13 collections.

Caligodes laciniatus, six females from two specimens (610–725 mm. BL). Mauritius; Zanzibar.

Lernanthropus tylosuri, 2 males and 10 females from 1 specimen (610 mm. BL). Mauritius.

Parabomolochus bellones, 4 males and 16 females from 6 specimens. Red Sea; Persian Gulf; Natal, South Africa.

Nothobomolochus gibber, one female from one specimen (311 mm. BL). Andaman Islands.

WEST AND CENTRAL PACIFIC

77 specimens (99–615 mm. BL) from 21 collections.

Caligodes laciniatus, three females from three specimens (305–470 mm. BL). Japan; Hawaii.

Lernanthropus tylosuri, 22 males and about 54 females from 16 specimens (295–615 mm. BL). Japan; Taiwan; Bikini, Marshall Islands; Philippine Islands; Hawaii.

Nothobomolochus gibber, 59 females from 29 specimens (192–374 mm. BL). Japan; Philippine Islands; Borneo; North Australia.

Parabomolochus bellones, five females from four specimens (286–449 mm. BL). Suruga Bay, Nagasaki, and Kobe, Japan; Djakarta, Java.

Parabomolochus sinensis, two females from one specimen (286 mm. BL). Djakarta, Java.

Colobomatus goodingi, 10 females from 9 specimens (226–278 mm. BL). Torres Strait, Australia.

Caligus sp. E, one male and five females from three specimens. Djakarta, Java; Torres Strait, Australia.

EASTERN PACIFIC

25 specimens (120–540 mm. BL) from 11 collections.

Caligodes laciniatus, 28 females from 8 specimens (252–540 mm. BL). Gulf of California; western Mexico; Cabo Blanco, Peru.

Lernanthropus tylosuri, 10 females and 17 males from 5 specimens (462–540 mm. BL). Gulf of California; western Mexico; Panama; Cabo Blanco, Peru.

FIGURE 172.—*Colobomatus goodingi* within preoperculomandibular canal of *Strongylura notata*. Note absence of inflammation in the wall of the canal, and flat epithelium. No changes in bone. Several disintegrating ova lie between the *Colobomatus* and the canal wall. X 55, H and E.

Parabomolochus constrictus, about 35 females from 9 specimens (128–483 mm. BL). Acapulco, Mexico; Panama Bay; Cabo Blanco, Peru.

Colobomatus goodingi, four females from interorbital canals of three specimens (465–540 mm. BL). Acapulco and Mazatlan, Mexico; Panama.

Belone belone (Linnaeus)

A large (maximum size 537 mm. BL, 743 mm. SL) eastern Atlantic species known from the White Sea, Norway, and Iceland south through the North Sea and the Baltic Sea along the coasts of France and Spain to Madeira, the Azores, and the Canary Islands. Also found throughout most of the Mediterranean and Black Seas.

77 specimens (105–537 mm. BL) from 47 collections.

Parabomolochus bellones, 40 females from under gill covers and oral valves of 21 specimens (163–318 mm. BL). Mediterranean Sea: Trieste; Venice; Naples; Tunisia.

Caligus belones, one female from inside the lower jaw posterior to the oral valve of one specimen (300 mm. BL). Elbe River.

Nothobomolochus gibber, one female from under the gill cover of one specimen (239 mm. BL). Funchal, Madeira.

FIGURE 173.—*Colobomatus goodingi* within preoperculomandibular canal of *Strongylura notata*. Marked inflammatory reaction surrounding area occupied by *Colobomatus* before the copepod dropped out when the tissue block was cut. Note new bone formation in zone of osteitis. Ostium of canal is at right. X 55, H and E.

Belone svetovidovi Collette and Parin

A medium-sized (maximum size 320 mm. BL, 445 mm. SL) marine species known from the Mediterranean Sea and the Atlantic Coast of Spain.

15 specimens (145–320 mm. BL) from 4 collections.

Parabomolochus bellones, one female from one specimen (210 mm. BL). Genoa Bay, Italy.

Nothobomolochus gibber, one male and three females from three specimens (171–210 mm. BL). Genoa Bay, Italy; Gabes, Tunisia.

Belonion apodion Collette
Belonion dibranchodon Collette

These are the two smallest species of needlefishes (maximum sizes 42 and 38 mm. BL, respectively). They are found in tributaries of the Amazon and Orinoco Rivers in Brazil, Venezuela, and Bolivia.

No copepods were found in any of the specimens of either species: *B. apodion*, 15 (22.6–41.8 mm. BL); *B. dibranchodon*, 7 (27.1–38.2).

Lhotskia gavialoides (Castelnau)

A large (maximum size 665 mm. BL, 955 mm. SL) Australian marine species.

24 specimens (162–665 mm. BL) from 8 collections.

Caligodes laciniatus, 22 females from about 7 specimens (292–665 mm. BL). New South Wales, Australia.

Parabomolochus bellones, 20 females from 8 specimens (228–297 mm. BL). Great Barrier Reef and New South Wales, Australia.

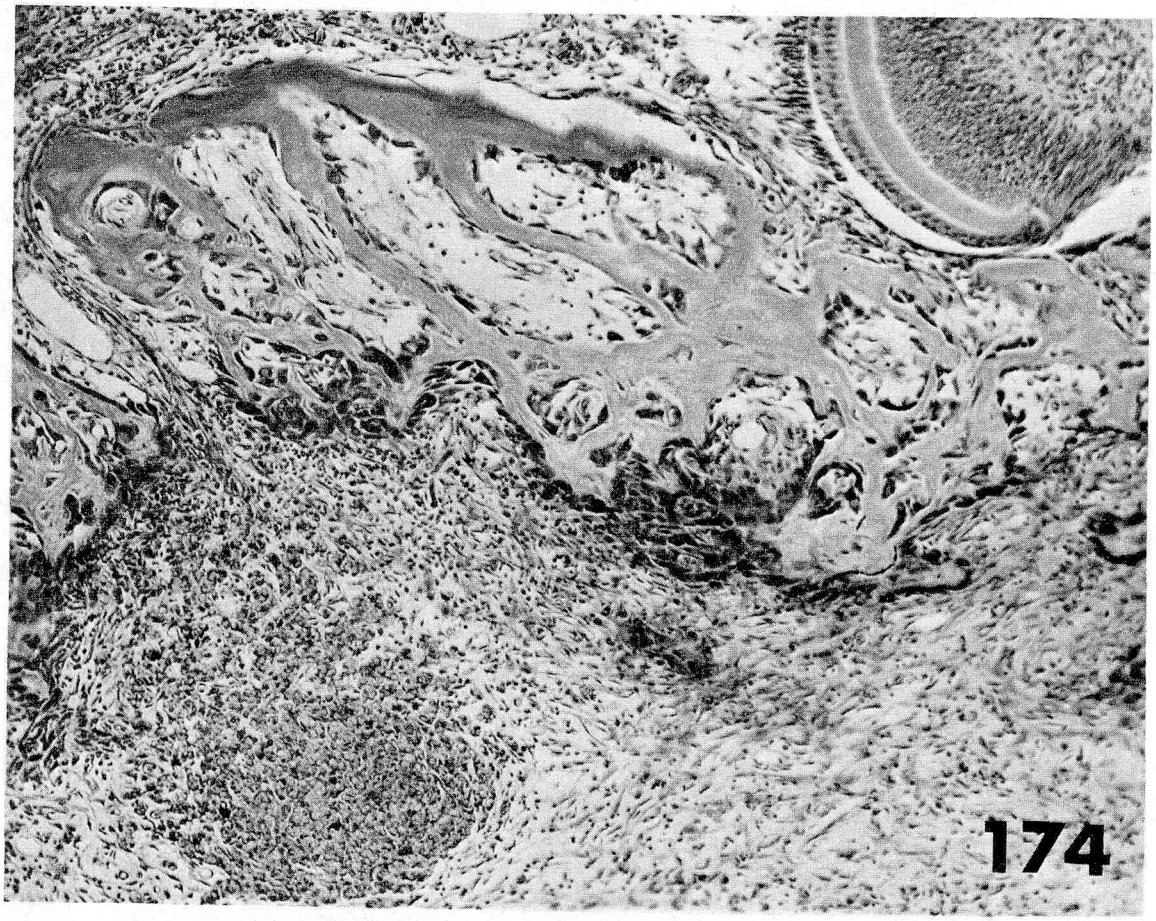


FIGURE 174.—*Colobomatus goodingi* within preoperculomandibular canal of *Strongylura notata*. A small granuloma adjacent to an area of new bone formation. Note hypertrophic osteoblasts at sites of bone formation. X 150, H and E.

Petalichthys capensis Regan

A medium-sized (maximum size 211 mm. BL) marine species known only from South Africa.

One specimen, 211 mm. BL.

No copepods.

Platybelone argalus (LeSueur)

A medium-sized (maximum size 300 mm. BL, 431+ mm. SL) polytypic worldwide marine species usually found around islands in tropical and subtropical seas (see fig. 176).

WESTERN ATLANTIC

146 specimens (90–248 mm. BL) from 31 collections.

Parabomolochus bellones, one male and 46 females from 15 specimens. Cay Arcas, Gulf of Mexico; Cuba; Puerto Rico; Cumana, Venezuela.

Caligus belones, one male and one female from two specimens. Cay Arcas, Gulf of Mexico; Navidad Bank, Caribbean Sea.

Lernanthropus belones, two males and one female from three specimens (164–248 mm. BL). Bermuda.

EASTERN ATLANTIC

129 specimens (144–287 mm. BL) from 21 collections around islands.

Caligus belones, many, mostly juveniles, from 54 specimens (161–287 mm. BL). Annobon, St. Helena, and Ascension Islands.

Lernanthropus tylosuri, one female from the gill filaments of one specimen. Fernando Póo.

Nothobomolochus gibber, two females from two specimens. Ascension and Annobon Islands.

INDIAN OCEAN

63 specimens (110–267 mm. BL) from 8 collections.

Nothobomolochus gibber, six females from three specimens (195–230 mm. BL). Aldabra Island.

Parabomolochus bellones, one female from one specimen (161 mm. BL). Saudi Arabia, Persian Gulf.

Caligodes laciniatus, one female from one specimen (198 mm. BL). Ari Atoll, Maldive Archipelago.

Caligus sp., six chalimus juveniles from pectoral fins of five specimens (184–231 mm. BL). Aldabra Island.

WEST AND CENTRAL PACIFIC

107 specimens (172–270 mm. BL) from 23 collections.

Nothobomolochus gibber, 149 females from about 57 specimens (174–238 mm. BL). Marshall, Tokelau, Christmas, Fanning, and Samoan Islands.

EASTERN PACIFIC

42 specimens (64–262 mm. BL) from 22 collections.

Parabomolochus constrictus, more than 65 females from 20 specimens. Baja California; Panama; Galapagos Islands; Guayaquil, Ecuador.

Caligus sp., from anal fin of one specimen (250 mm. BL). Baja California.

Potamorrhaphis guianensis (Schomburgk)

A small (maximum size 157 mm. BL, 232+ mm. SL) fresh-water species of eastern South America (see fig. 180).

63 specimens (67–157 mm. BL) from 13 collections.

Ergasilus orientalis, nine females from gill filaments of six specimens (115–157 mm. BL). Gurupá, near mouth of Amazon River, Brazil.

Pseudotylosurus angusticeps (Günther)

A medium-sized (maximum size 255 mm. BL, 379 mm. SL) South American fresh-water species (see fig. 180).

25 specimens (98–243 mm. BL) from 10 collections.

Acusicola cumula, eight females from gill filaments of two specimens. Amazon drainage, Brazil.

Strongylura anastomella (Valenciennes)

A large (maximum size 580 mm. BL, 805 mm. SL) marine species found in the northwestern Pacific—the Sea of Japan, Japan, Korea, and Formosa (see fig. 179).

33 specimens (128–580 mm. BL) from 18 collections.

Lernanthropus tylosuri, 10 males and 55 females from 15 specimens (285–580 mm. BL [average 390]). Japan; U.S.S.R.; Korea.

Lernanthropus belones, two females and six immature females from one specimen (430 mm. BL). Suruga Bay, Japan.

Parabomolochus bellones, 55 females from 14 specimens (227–474 mm. BL [average 344]). Japan; U.S.S.R.

Caligus sp., one female from one specimen. Boshu, Japan.

Strongylura exilis (Girard)

A large (maximum size 490 mm. BL, 715+ mm. SL) eastern Pacific marine species found from southern California to Peru and the Galapagos Islands (see fig. 179). Most closely related to the western Atlantic *S. marina*.

97 specimens (54–490 mm. BL) from 30 collections.

Parabomolochus ensiculus, 14 females from under oral valves of 13 specimens (89–363 mm. BL). San Diego, Calif.; Baja California; Chame Point, Panama; Peru.

Parabomolochus constrictus, 20 females from 9 specimens (155–367 mm. BL). Baja California; northern Peru.

Lernanthropus belones, 43 males and 64 females from 14 specimens (112–363 mm. BL). San Diego, Calif.; Baja California.

Lernanthropus tylosuri, three males and five females from four specimens (227–340 mm. BL). Baja California; northern Peru.

Colobomatus goodingi, one female from one specimen (415 mm. BL). Miraflores Lock, Canal Zone, Panama.

Caligus sp., one male from the mouth of one specimen (142 mm. BL). Gulf of Nicoya, Costa Rica.

Strongylura fluviatilis (Regan)

A medium-sized (maximum size 321 mm. BL, 517 mm. SL) fresh-water species found in the rivers of Ecuador and Colombia.

33 specimens (104–321 mm. BL) from 10 collections.

Ergasilus argulus, 58 females from gill filaments of 4 specimens (153–196 mm. BL). Dagua River mouth, Colombia.

Strongylura incisa (Valenciennes)

A medium-sized (maximum size about 450 mm. BL) marine species found from Ceylon, Malaysia, and Thailand through the Philippine Islands to the Marshall Islands, Gilbert Islands, Marianas Islands, Samoan Islands, Fiji Islands, and Palau Islands (see fig. 179).

75 specimens (59–450 mm. BL) from 42 collections.

Lernanthropus belones, 6 males and 10 females from 7 specimens (193–450 mm. BL). Marshall Islands; Gilbert Islands; Philippine Islands; Arnhem Land, Australia; Singapore.

Lernanthropus tylosuri, one female from one specimen (233 mm. BL). Great Barrier Reef, Australia.

Parabomolochus bellones, six females from two specimens (102–222 mm. BL). Philippine Islands.

Ergasilus orientalis, 19 females from 1 specimen (220 mm. BL). Emerald River at and near mouth, Arnhem Land, Australia.

Caligus sp. D, two females from two specimens (233–315 mm. BL). Great Barrier Reef, Australia; Philippine Islands.

Strongylura krefftii (Günther)

A medium-sized (maximum size 388 mm. BL, 735 mm. SL) fresh-water species found in northern Australia—Arnhem Land and Queensland.

44 specimens (21–388 mm. BL) from 7 collections.

Ergasilus semicoleus, 36 females on gill filaments of 6 specimens (207–325 mm. BL).

Large billabong at Oenpelli, Arnhem Land, Northern Territory, Australia.

Strongylura leiura (Bleeker)

A large (maximum size 501 mm. BL, 790 mm. SL) marine species most closely related to *S. anastomella*. Found from east Africa, the Persian Gulf, and India to Borneo, the Philippines, Australia, China, and Fiji (see fig. 179).

49 specimens (115–398 mm. BL) from 35 collections.

Caligoides laciniatus, 39 females from 5 specimens (171–313 mm. BL). Pondicherry, India; Philippine Islands; Formosa.

Lernanthropus tylosuri, four females from three specimens (171–280 mm. BL). Persian Gulf; Philippine Islands.

Nothobomolochus digitatus, five females from four specimens (171–229 mm. BL). Java; Gulf of Thailand; Philippine Islands.

Parabomolochus bellones, one female from oral valve of one specimen (387 mm. BL). Hong Kong.

Strongylura marina (Walbaum)

A medium-sized (maximum size 418 mm. BL, 640 mm. SL) marine species found in the western Atlantic from Massachusetts south to Rio de Janeiro (see fig. 179). Not found in the Bahamas or Antilles. Frequently runs long distances up freshwater rivers.

316 specimens (43–418 mm. BL) from 100 collections.

Parabomolochus bellones, 3 males and 116 females from 53 specimens (55–300 mm. BL [average 149.5]). Massachusetts; North Carolina; Georgia; Key West; Everglades; western Florida; Yucatan; Panama; Trinidad; Venezuela.

Colobomatus goodingi, six females from cephalic lateral line canals of five or six specimens (171–260 mm. BL [average 216.8]). Clearwater, Fla., Everglades, Fla., western Florida.

Lernanthropus belones, 114 males and 58 females from 37 specimens (110–280 mm. BL). Beaufort, N.C.; St. Simons and Jekyll Islands, Ga.; Lemon Bay, Alligator Harbor, Clearwater, and Amelia River, Fla.; Trinidad; Venezuela.

Lernanthropus tylosuri, three males and two females from three specimens (296–410 mm. BL). Belize, British Honduras.

Lerneaolophus sultanus, one female from one specimen (368 mm. BL). Belize, British Honduras.

Ergasilus sp. A, one female from one specimen (418 mm. BL). Lake Yzabel, Guatemala.

Acusicola tenax, 203 females from 18 specimens (113–285 mm. BL). Usumacinta River, El Petén, Guatemala.

Ergasilus spatulus, 23 females from 5 specimens (129–272 mm. BL). Lake Pontchartrain, La.; Tortuguero, Costa Rica.

Argulidae, from one specimen, (230 mm. BL). Lake Pontchartrain, La.

Strongylura notata (Poey)

A medium-sized (maximum size 245 mm. BL, 411 mm. SL) western Atlantic marine species

found from southern Florida and the Bahamas to Cuba, Jamaica, Yucatan, and Honduras (see fig. 179).

About 200 specimens (29–245 mm. BL) from about 50 collections.

Colobomatus goodingi, from cephalic lateral line canals of 42 specimens (72–238 mm. BL [average 133.3]). Bimini, Bahamas; Tampa Bay, Cape Haze, Sanibel Island, and Key Biscayne, Fla.; Providence Island, Caribbean Sea.

Lernanthropus belones, 63 males and 78 females from about 50 specimens (87–245 mm. BL [average 151.0]). Bimini and Andros Is., Bahamas; Sanibel Island, Cape Haze, Sarasota, Pensacola, and Key Biscayne, Fla.; Florida Keys; Cuba; Jamaica; Yucatan.

Parabomolochus bellones, 3 males and 158 females from about 50 specimens (41–226 mm. BL [average 108.4]). Andros Island, Bahamas; Cape Haze, Sarasota, New Smyrna, Pensacola, Bayport, and Key Biscayne, Fla.; Florida Keys; Jamaica; Yucatan and Tampico, Mexico.

Caligus sp. B, four females from two specimens. Sarasota, Fla.

Strongylura scapularis (Jordan and Gilbert)

A medium-sized (maximum size 245 mm. BL, 385 mm. SL) eastern Pacific marine species found from Costa Rica to Ecuador (see fig. 179).

38 specimens (36–245 mm. BL) from 12 collections.

Lernanthropus belones, eight males and four females from four specimens (157–227 mm. BL). Canal Zone, Panama; Guyaquil, Ecuador.

Parabomolochus constrictus, 15 females from under opercles of about 7 specimens (64–148 mm. BL). Costa Rica; Canal Zone, Panama.

Parabomolochus ensiculus, 139 females from under oral valves of 21 specimens (59–235 mm. BL). Canal Zone, Panama; Ecuador; Peru.

Ergasilus argulus, 48 females from gill filaments of 6 specimens (187–245 mm. BL). Mouth of Dagua River, Colombia.

Strongylura senegalensis (Valenciennes)

A medium-sized (maximum size 263 mm. BL, 381 mm. SL) eastern Atlantic marine species found from Senegal through the Gulf of Guinea to Angola (see fig. 179). Sometimes enters rivers.

27 specimens (116–229 mm. BL) from 6 collections.

Parabomolochus bellones, five females from five specimens (143–175 mm. BL). Volta River at Ada, Ghana; Ebzie Lagoon, Ivory Coast.

Ergasilus inflatipes, 62 females from 17 specimens (129–218 mm. BL). Volta River at Ada, Ghana; Ebzie Lagoon, Ivory Coast.

Strongylura strongylura (van Hasselt)

A medium-sized (maximum size 233 mm. BL, 366+ mm. SL) estuarine species found along the coasts of India, southeast Asia, China, Borneo, the Philippines, and Australia (see fig. 179).

69 specimens (56–233 mm. BL) from 32 collections.

Parabomolochus bellones, two females from one or two specimens. Arnhem Land, Australia.

Parabomolochus sinensis, 12 females and 1 male from 7 specimens (78–166 mm. BL). Hong Kong; Amoy and Fukien, China; Penang, Malaysia.

Nothobomolochus digitatus, 19 females from 12 specimens (103–206 mm. BL). Bombay and Calicut, India; Penang, Malaysia; Hong Kong; Arnhem Land, Australia.

Lernanthropus belones, 11 males and 10 females from 9 specimens (145–255 mm. BL). Madras and Bombay, India; China; Singapore; Philippine Islands.

Lernanthropus tylosuri, two males and three females from six specimens (103–201 mm. BL). Penang, Malaysia.

Ergasilus coleus, 28 females from gill filaments of 6 specimens. Cagayan de Misamis, Mindanao, Philippine Islands; Sandakan Bay, Borneo; Porto Novo, Madras, India.

Strongylura timucu (Walbaum)

A medium-sized (maximum size 275 mm. BL, 418 mm. SL) western Atlantic marine species found in southern Florida, the West Indies, Central and South America south to Rio de Janeiro (see fig. 179). Frequently enters fresh water.

281 specimens (82–250 mm. BL) from 95 collections.

Colobomatus goodingi, 31 females from cephalic lateral line canals of 26 specimens (112–232 mm. BL [average 158.0]). Sarasota, Fla.;

Florida Keys; Haiti; Puerto Rico; Virgin Islands; Curaçao.

Lernanthropus belones, 76 males and 123 females from 72 specimens (93–250 mm. BL [average 170.9]). Bahamas; Cedar Keys, Lemon Bay, Sarasota, Clearwater, and Key Biscayne, Fla.; Cuba; Jamaica; Puerto Rico; Virgin Islands; Yucatan; Panama; Rio de Janeiro, Brazil.

Lernanthropus tylosuri, six males and seven females from one specimen (235 mm. BL). Rio de Janeiro, Brazil.

Parabomolochus bellones, about 22 males and 150 females from 80 specimens (49–250 mm. BL [average 158.2]). Everglades, Tampa Bay, Clearwater, Lemon Bay, Sarasota, Pensacola, Sanibel Island, and Key Biscayne, Fla.; Yucatan; Jamaica; Haiti; Puerto Rico; Virgin Islands.

Ergasilus spatulus, six females from four specimens (125–250 mm. BL). Tortuguero, Costa Rica.

Strongylura urvillii (Valenciennes)

A medium-sized (maximum size, 228 mm. BL, 386 mm. SL) western Pacific marine species known from the Philippines, New Hebrides, and East Indies (see fig. 179).

21 specimens (79–220 mm. BL) from 11 collections.

Lernanthropus tylosuri, one male from one specimen (136 mm. BL). Culion, Philippine Islands.

Caligus sp. D, one female from one specimen (220 mm. BL). Verde del Sur Island, Philippine Islands.

Parabomolochus bellones, one female from one specimen (168 mm. BL). Manila, Luzon, Philippine Islands.

Ergasilus coleus, four females from gill filaments of one specimen (130 mm. BL). Culion, Philippine Islands.

Tylosurus acus (Lacépède)

A large (maximum size 950 mm. BL, 1,285 mm. SL) worldwide polytypic marine species of tropical and subtropical waters (see fig. 177).

WESTERN ATLANTIC

***T. acus acus* (Lacépède)**

39 specimens (110–950 mm. BL) from 26 collections.

Caligodes laciniatus, 40 females and 1 male from oral valves of 17 specimens (178–516 mm. BL). Virginia; Florida; Bahamas; Gulf of Mexico; British Honduras; Haiti; Virgin Islands.

Lernanthropus tylosuri, three females and two males from gill filaments of three specimens (338–382 mm. BL). British Honduras; Puerto Rico; Virgin Islands.

Parabomolochus bellones, seven females and three males from four specimens (200–305 mm. BL). Florida; Gulf of Mexico; British Honduras.

Colobomatus goodingi, 10 females from 8 specimens (244–400 mm. BL). North Carolina; Gulf of Mexico; Bahamas; British Honduras.

Lernaeolophus sultanus, two females from roof of upper jaw of one head. Haiti.

MEDITERRANEAN SEA

***T. acus imperialis* (Rafinesque)**

23 specimens (200–443 mm. BL) from 5 collections. No copepods.

GULF OF GUINEA

***T. acus rafale* Collette and Parin**

21 specimens (201–570 mm. BL) from 15 collections.

Caligodes laciniatus, 15 females from 10 specimens (261–456 mm. BL). Freetown, Sierra Leone; Congo; Angola.

Lernanthropus tylosuri, a few males and about 15 females from 6 specimens (261–570 mm. BL). Freetown, Sierra Leone; Luanda, Lobito, and Baía Farta, Angola.

Parabomolochus bellones, four females from three specimens (240–356 mm. BL). Freetown, Sierra Leone; Congo.

Colobomatus goodingi, six females from three specimens (452–570 mm. BL). Lobito and Baía Farta, Angola.

Caligus sp. A, one female from one specimen (201 mm. BL). Freetown, Sierra Leone.

INDIAN OCEAN

***T. acus melanotus* (Bleeker)**

One specimen (342 mm. BL).

Caligodes laciniatus, several females from one specimen (342 mm. BL).

WESTERN AND CENTRAL PACIFIC

***T. acus melanotus* (Bleeker)**

33 specimens (281–610 mm. BL) from 21 collections.

Caligodes laciniatus, nine females from six specimens (415–610 mm. BL). Philippine Islands; Nagasaki, Japan; Hawaii.

Lernanthropus tylosuri, two males and two females from four specimens (384–463 mm. BL). Djakarta, Java; Philippine Islands.

Colobomatus goodingi, one female from preorbital canal of one specimen (415 mm. BL). Jolo, Philippine Islands.

Caligus tylosuri, one male and one female from under gill covers of two specimens (301–416 mm. BL). Luzon, Philippine Islands; Sea of Japan.

Nothobomolochus gibber, one female from one specimen (380 mm. BL). Taiwan.

EASTERN PACIFIC

***T. acus pacificus* (Steindachner)**

30 specimens (50–550 mm. BL) from 22 collections.

Caligodes laciniatus, nine females from four specimens (308–535 mm. BL). Revillagigedos Islands, Mexico; Piñas Bay, Panama; Cabo Blanco, Peru.

Lernanthropus tylosuri, 7 males and 19 females from 6 specimens (296–535 mm. BL). Revillagigedos Islands; Gulf of California; Acapulco, Mexico; Piñas Bay, Panama.

Parabomolochus constrictus, about 31 females from 8 specimens (112–339 mm. BL). Costa Rica; Panama; Colombia; Peru.

Colobomatus goodingi, five females from three specimens (296–535 mm. BL). Acapulco, Mexico; Piñas Bay, Panama; Cabo Blanco, Peru.

Caligus tylosuri, one male from dorsal fin of one specimen (470 mm. BL). Bahia Palmas, Gulf of California.

Caligus sp. B, one female from one specimen (316 mm. BL). Cabo Blanco, Peru.

Caligus sp. C, two females from the throat of one specimen (535 mm. BL). Piñas Bay, Panama.

Tylosurus choram (Rüppell)

A medium-sized (maximum size at least 415 mm. BL, 625 mm. SL) Indo-West Pacific species of marine needlefish.

Two specimens (250–260 mm. BL) from the Persian Gulf, 14 (95–415 mm. BL) from the Red Sea, 1 from the Seychelles Islands, and 1 from the eastern Mediterranean Sea (277 mm. BL).

Caligodes laciniatus, seven females from four specimens (277–400 mm. BL). Red Sea; Seychelles Islands.

Lernanthropus tylosuri, one female from one specimen (415 mm. BL). Red Sea.

Caligus sp. D, one female from one specimen (261 mm. BL). Red Sea.

Tylosurus crocodilus (Peron and Le Sueur)

A large (maximum size 860 mm. BL, 1,156 mm. SL) worldwide polytypic marine species of tropical and subtropical waters (see fig. 178).

WESTERN ATLANTIC

38+ specimens (88–480 mm. BL) from 19+ collections.

Caligodes laciniatus, 19 females from 7 specimens (205–480 mm. BL). Florida; Cuba; Jamaica; Trinidad; Venezuela.

Lernanthropus tylosuri, 40 females and 39 males from 20 specimens (135–420 mm. BL). Matecumbe Key, Fla.; Bahamas; Venezuela.

Parabomolochus bellones, 12 females and 5 males from 8 specimens (135–244 mm. BL). Virginia Key and Sarasota, Fla.; Havana, Cuba; Venezuela.

Colobomatus goodingi, 23 females from 18 specimens (180–477 mm. BL). Virginia Key, Fla.; Bahamas; Trinidad; Venezuela.

Caligus sp., four chalimus from fins of three specimens (112–235 mm. BL). Key Biscayne, Fla.; Golfo de Cariaco, Venezuela.

Argulidae, from one specimen. Sarasota, Fla.

GULF OF GUINEA

Four specimens (173–284 mm. BL) from four collections.

Caligodes laciniatus, one female from one specimen (284 mm. BL). Liberia.

Lernanthropus tylosuri, four females from one specimen (173 mm. BL). Fernando Póo.

Colobomatus goodingi, seven females from one specimen (215 mm. BL). Cameroons.

INDIAN OCEAN

70 specimens (72–500 mm. BL) from 45 collections.

Caligodes laciniatus, 54 females from 20 specimens (172–490 mm. BL). Seychelles and Comores Islands; Aldabra; Zanzibar; Madagascar; Mauritius; Gulf of Aden; Arabian Gulf; Persian Gulf; Gulf of Mannar, Ceylon.

Lernanthropus tylosuri, 11 males and 23 females from 16 specimens (172–450 mm. BL). Madagascar; Mauritius; Zanzibar; Kenya; Seychelles; Red Sea; Gulf of Aden; Arabian Gulf; Persian Gulf; Kerala, India; Ceylon.

Parabomolochus bellones, eight females from four specimens (175–217 mm. BL). Mozambique; Kenya; Kerala, India; Moscos Islands, Burma.

Nothobomolochus gibber, 10 females from 6 specimens (98–233 mm. BL). Madagascar; Zanzibar; Seychelles Islands; Red Sea; Kerala, India.

Colobomatus goodingi, 12 females from 10 specimens (157–446 mm. BL). Madagascar; Red Sea; Gulf of Aden; Kerala, India; Gulf of Mannar, Ceylon.

Caligus sp., seven juveniles on fins of three specimens (72–142 mm. BL). Shimoni, Kenya.

Caligus sp., one male in mouth of one specimen (105 mm. BL). Nosy Bé, Madagascar.

WESTERN AND CENTRAL PACIFIC

76 specimens (58–570 mm. BL) from 51 collections.

Caligodes laciniatus, 28 females from 6 specimens (254–565 mm. BL). Thailand; Singapore; Samoa; Philippine Islands; Hawaii.

Lernanthropus tylosuri, 14 males and 33 females from 15 specimens (150–440 mm. BL). Japan; Thailand; Singapore; Philippine Islands; Java; Borneo; Marshall Islands; Hawaii.

Nothobomolochus gibber, two females from two specimens (190–286 mm. BL). Bellona Island, Solomon Islands; Cavite, Philippine Islands.

Nothobomolochus pacificus, one female from one specimen (388 mm. BL). Sandakan, North Borneo.

Colobomatus goodingi, nine females from seven specimens (214–420 mm. BL). Java; Philippine Islands; Marianas Islands; Solomon Islands.

Caligus tylosuri, four females from two specimens (317–388 mm. BL). Leyte, Philippine Islands; Sandakan, North Borneo.

Lernaeenicus sp., one female from one specimen (252 mm. BL). Manila, Philippine Islands.

EASTERN PACIFIC

T. crocodilus fodiator Jordan and Gilbert

24 specimens (65–671 mm. BL) from 11 collections.

Caligodes laciniatus, 26 females from 6 specimens (262–450 mm. BL). Mexico; Cocos Islands; Panama Canal Zone.

Lernanthropus tylosuri, 2 males and 19 females from 5 specimens (303–515 mm. BL). Mazatlan, Mexico; Panama Canal Zone.

Parabomolochus constrictus, 12 females from 8 specimens (69–450 mm. BL). Mexico; Cocos Islands; Panama Canal Zone.

Colobomatus goodingi, six females from three specimens (161–570 mm. BL). Cocos Islands; Panama Canal Zone.

Caligus sp. C, one female from one specimen (535 mm. BL). Panama Canal Zone.

Tylosurus punctulatus (Günther)

A medium-sized (maximum size 385 mm. BL, 573 mm. SL) western Pacific marine species. Known from Malaya, the Philippines, Borneo, New Guinea, the Celebes, Australia, and the Solomon Islands.

31 specimens (87–385 mm. BL) from 22 collections.

Lernanthropus tylosuri, two females from two specimens (180–205 mm. BL). Culion and Luzon, Philippine Islands.

Lernanthropus belones, four females and one male from three specimens (235–269 mm. BL). Sandakan, North Borneo.

Nothobomolochus digitatus, three females from two specimens (110–130 mm. BL). New Guinea.

Xenentodon cancila (Hamilton-Buchanan)

A small (maximum size 169 mm. BL, 284 mm. SL) fresh-water species found in India, Ceylon, and southeast Asia (see fig. 180).

65 specimens (56–169 mm. BL) from 13 collections.

Ergasilus coleus, 51 females from gill filaments of 5 specimens (66–112 mm. BL). Travancore and Calcutta, India.

Paraergasilus remulus, three females from operecula of two specimens (111–112 mm. BL). Prek Andhor, Cambodia.

Ergasilus sp., one female from gill filaments of one specimen (119 mm. BL). Ceylon.

Ergasilidae, one female from gill filaments of one specimen (102 mm.). Sutlej River, Punjab, India.

Lernea sp., one female from behind left pectoral fin of one specimen. Locality unknown.

LITERATURE RECORDS OF NEEDLEFISH COPEPODS

As stated previously, we did not incorporate literature records into the data included in this paper. Because of the comprehensive nature of our collections we felt that they would add nothing of significance and might even add data based on misidentified parasites or hosts. To complete this report on needlefish copepods, however, we felt it desirable to cite those reports here (a few have already been cited elsewhere in this paper). We consider most of the recent records to be accurate. The records are listed by recorded host. Wherever possible we have included the corrected host or parasite name in parentheses.

***Ablennes anastomella* (=*Strongylura anastomella*)**

Lernanthropus cornutus: Shiino, 1965 (Japan; = *L. tylosuri*).

Ablennes hians

Bomolochus tumidus Shiino, 1959 (Sea of Japan; = *Nothobomolochus gibber*).

Pseudopetalus caudatus var. *rotundus* Pillai, 1962 (Trivandrum, S. India).

Lernanthropus cornutus: Shiino, 1965 (Japan; = *L. tylosuri*).

Caligodes laciniatus: Pillai, 1961 (Trivandrum, S. India); Nuñes-Ruivo, 1962a, 1962b (Baie de Moçâmedes, Angola).

***Belone acus* (=*B. belone*)**

Bomolochus belones: Brian, 1902 (Elba Island, Italy); Richiardi, 1880 (Italy); (=*Parabomolochus bellones*).

***Belone almeida* (=*Strongylura marina* or *S. timucu*)**

Lernanthropus belones Krøyer, 1863 (Brazil).

***Belone ardeola* (= *Strongylura marina*?)**

Bomolochus ardeolae Krøyer, 1863 (New Orleans, La.).

Artacolax ardeolae: Wilson, 1911 (= *B. ardeolae*).

***Belone bellone* (= *B. belone*)**

Parabomolochus bellones: Vervoort, 1962 (Holland).

Caligus belones: Delamare Deboutteville and Nuñes-Ruivo, 1958 (Mediterranean coast of France).

***Belone contrainii* (sic) (= *Tylosurus acus imperialis*)**

Caligodes laciniatus: Brian, 1902 (Genoa, Italy).

***Belone rostrata* (= *B. belone*)**

Bomolochus belones: Valle, 1880 (Adriatic Sea; = *Parabomolochus bellones*).

***Belone vulgaris* (= *B. belone*)**

Bomolochus bellones: Hartmann, 1870 (Mediterranean Sea); Brian, 1906 (Helgoland, Germany); (= *Parabomolochus bellones*).

Caligus belones Krøyer, 1863 (Denmark).

Metopocatacoteinus hirsutus Hesse, 1872 (France; = *Parabomolochus bellones*).

***Belone* Sp. (=*Strongylura* or *Tylosurus* Sp.)**

Sciaenophilus laciniatus Krøyer, 1863 (Mollucca Islands; =*Caligodes laciniatus*).

Caligodes laciniatus: Heller, 1868 (Indian Ocean).

***Belones* (sic) *platyura* (=*Platybelone argalus*)**

Nothobomolochus gibber: Lewis, 1968 (Eniwetok Atoll, Marshall Islands).

***Esox bellone* (=*Belone belone*)**

Bomolochus bellones Burmeister, 1833 (Helgoland, Germany).

***Lepisosteus osseus* (=*Tylosurus acus*?)**

Caligodes megacephalus Wilson, 1905 (Woods Hole, Mass.; =*C. laciniatus*).

***Strongylura acus* (=*Tylosurus acus*)**

Caligus schistonyx: Pearse, 1947 (3 chalimi; Beaufort, N.C.; = ?).

***Strongylura crocodila* (=*Tylosurus acus*?)**

Caligodes laciniatus: Capart, 1953 (Dakar); Capart, 1959 (Congo).

Lernanthropus cornutus: Capart, 1953 (Gorée, Sénégal); Delamare Deboutteville and Nuñes-Ruivo, 1954 (Gorée); (=*L. tylosuri*).

Strongylura leiura

Caligodes laciniatus: Kirtisinghe, 1937 (Ceylon).

Lernanthropus cornutus Kirtisinghe, 1937 (Ceylon; =*L. tylosuri*).

Strongylura notata

Lernanthropus chlamydotes: Bere, 1936 (Lemon Bay, Fla.; = *L. belones*).

Strongylura strongylura

Caligodes laciniatus: Kirtisinghe, 1937 (Ceylon).

Strongylura timucu (=*S. marina*?)

Bomolochus nitidus: Bere, 1936 (Lemon Bay, Fla.; =*Parabomolochus bellones*).

Lernanthropus chlamydotes: Bere, 1936 (Lemon Bay, Fla.; =*L. belones*).

Tylosurus acus

Tuxophorus caligodes Wilson, 1908 (chalimus: Beaufort, N.C.).

Tylosurus crocodilus

Caligus tylosuri: Pillai, 1961 (Vizhingom, S. India).

Caligus malabaricus Pillai, 1961 (Trivandrum, S. India).

Caligoides laciniatus: Pillai, 1961 (Trivandrum, S. India).

Lernanthropus cornutus Kirtisinghe, 1937 (Ceylon; =*L. tylosuri*).

Tylosurus giganteus (=*T. crocodilus*)

Bomolochus gibber Shiino, 1957 (Owase, Japan; =*Nothobomolochus gibber*).

Tylosurus imperialis (=*T. acus imperialis*)

Lernanthropus tylosuri Richiardi, 1880, 1885 (Italy).

Caligodes laciniatus: Brian, 1906 (Genoa, Italy).

Tylosurus incisus (=*Strongylura incisa*)

Lernanthropus cornutus: Kabata, 1962 (Gilbert and Ellice Islands; = *L. tylosuri*).

Tylosurus indicus (=*T. crocodilus*)

Nothobomolochus gibber: Vervoort, 1962 (Japan; based on Shiino, 1957).

Tylosurus marinus (=*Strongylura marina*)

Lepeophtheirus edwardsi: Wilson, 1905 (male; Woods Hole, Mass.); Wilson, 1908 (Beaufort, N.C.).

Tuxophorus caligodes Wilson, 1908 (8 chalimi; Beaufort, N.C.).

Bomolochus concinnus Wilson, 1911 (Beaufort, N.C.;=*Parabomolochus bellones*).

Lernanthropus chlamydotes Wilson, 1922 (Beaufort, N.C.;=*L. belones*).

Lernanthropus sp.: Linton, 1905 (Beaufort, N.C.; =*L. belones*).

Tylosurus schistomatorhynchus (=*Ablennes hians*)

Lernanthropus chlamydotes: Yamaguti, 1939b (Japan;=*L. tylosuri*).

Tylosurus strongylurus (=*Strongylura strongylura*)

Tuxophorus tylosuri Rangnekar, 1956 (Bombay;= *Caligus tylosuri*).

Caligodes laciniatus: Rangnekar, 1959 (Bombay).

HOST-PARASITE RELATIONSHIPS

Host Specificity

To answer the question, "Are needlefish copepods host specific?" we compared statistically the percentage infestation of the various species of needlefishes by different species of copepods. The analysis yielded little evidence of host specificity in the copepods of fresh-water needlefishes—the Ergasilidae (table 3). Rather, a given species of ergasilid is found on the fresh-water needlefishes in its range. Most ergasilids found on needlefishes are restricted to one host species because it is the only one available. When there are more hosts, they are utilized. *Ergasilus spatulus* is present on both *Strongylura marina* and *S. timucu* at Tortuguero, Costa Rica, but on only *S. marina* in Lake Pontchartrain, La., where it is the only needlefish present. *E. argulus* is found on *S. fluviatilis*, a fresh-water South American species of needlefish and also on *S. scapularis*, primarily a marine species, but taken with *S. fluviatilis* at the mouth of the Dagua River, Colombia. *E. coleus* was collected at several localities from *S. strongylura*, *S. urvillii*, and *Xenentodon cancila*. *X. cancila* is a fresh-water species, *S. strongylura* an estuarine species, and *S. urvillii* a primarily marine species.

The worldwide species of needlefishes (table 4) differ sharply in infestation between *Ablennes hians*, *Tylosurus acus*, and *T. crocodilus* on the one hand, and *Platybelone argalus* on the other.

TABLE 3.—*Percentage of specimens of 12 fresh-water species of needlefishes (or fresh-water populations of marine species of* Strongylura) *infested by 11 species of ergasilid copepods*

Area, species, and number of specimens	*Ergasilus*								*Acusicola*		*Paraergasilus*
	spatulus	*argulus*	*coleus*	*semicoleus*	*inflatipes*	*orientalis*	sp. A	sp. B	*tenax*	*cunula*	*remulus*
	Percent										
North America:											
S. marina (190)	3	----	----	----	----	----	0.5	----	9	----	--------
S. timucu (18)	22	----	----	----	----	----	6	----	----	----	--------
South America:											
S. fluviatilis (33)	----	12	----	----	----	----	----	----	----	----	--------
S. scapularis (7)	----	86	----	----	----	----	----	----	----	----	--------
Potamorrhaphis (63)	----	----	----	----	----	10	----	----	----	----	--------
Pseudotylosurus (25)	----	----	----	----	----	----	----	----	----	8	--------
Africa:											
S. senegalensis (27)	----	----	----	----	59	----	----	----	----	----	--------
Asia:											
S. incisa (8)	----	----	----	----	----	13	----	----	----	----	--------
S. krefftii (44)	----	----	----	14	----	----	----	----	----	----	--------
S. strongylura (10)	----	----	50	----	----	----	----	----	----	----	--------
S. urvillii (3)	----	----	33	----	----	----	----	----	----	----	--------
Xenentodon (65)	----	----	8	----	----	----	----	2	----	----	3

TABLE 4.—*Percentage of specimens of four worldwide species of needlefishes infested by 10 species of copepods*

Species, area, and number of specimens	*Parabomolochus*			*Nothobomolochus*		*Caligodes laciniatus*	*Lernanthropus*		*Colobomatus goodingi*	*Caligus* spp.
	bellones	*constrictus*	*ensiculus*	*gibber*	*digitatus*		*tylosuri*	*belones*		
	Percent									
Ablennes hians;										
W. Atlantic (81)	38					2	0.5	0.1	0.2	
Gulf of Guinea (37)	46					24	11		41	11
Indian Ocean (31)	19			3		8	3			
W. Central Pacific (77)	5			38		3	21		12	4
E. Pacific (25)		36				32	20		12	
Tylosurus acus;										
W. Atlantic (39)	10					44	8		21	
Mediterranean (23)										
Gulf of Guinea (21)	14					48	29		14	5
Indo-W. Pacific (34)						24	9		3	6
E. Pacific (30)		27				10	20		10	10
Tylosurus crocodilus;										
W. Atlantic (38)	21					18	53		47	5
Gulf of Guinea (4)						25	25		25	
Indian Ocean (70)	6			9		29	21		14	6
W. Central Pacific (76)				3	1	8	20		9	3
E. Pacific (24)		33				25	21		13	4
Platybelone argalus;										
W. Atlantic (146)	10							1		1
E. Atlantic (129)				2			.8			42
Indian Ocean (62)	2			5		2				8
W. Central Pacific (107)				53						
E. Pacific (46)		43								

Three species of copepods are common on the first three species of needlefishes: *Caligodes laciniatus*, *Lernanthropus tylosuri*, and *Colobomatus goodingi*. There are only a few accidental records of *Caligodes* and *Lernanthropus* from *Platybelone* and none at all of *Colobomatus*. Yet all four species of needlefishes are commonly infested with *Parabomolochus bellones* or its eastern Pacific analog *P. constrictus*. Collette (in Collette and Parin, 1970) considered *Ablennes* and *Tylosurus* as closely related; the high incidence of *Caligodes*, *L. tylosuri*, and *Colobomatus* infestation in these genera could be considered as parasitological support for this view. Parin (in Collette and Parin, 1970), however, considered the similarities between *Ablennes* and *Tylosurus* as convergent evolution associated with occupation of a similar ecological niche. The parasitological data could be equally well applied to the support of this point of view.

Examination of the copepods associated with 16 other marine species of needlefishes (table 5) may help in deciding between the alternatives. *Caligodes* is found on one of the two other species of *Tylosurus*—*T. choram*. *Caligodes* is also found on *Lhotskia gavialoides*, a species placed in *Tylosurus* by Collette and Berry (1965) but referred to the monotypic *Lhotskia* by Parin (1967). The sixth species infested with *Caligodes*, *Strongylura leiura*, is the only member of its genus to be so infested. *S. leiura* is definitely not closely related to *Ablennes* or *Tylosurus*. Its only characters in common with the other *Caligodes* hosts are: large size (501 mm. BL compared to 665–950 mm. BL), wide distribution, and apparent intolerance of estuarine conditions. Thus, we conclude that *Caligodes* is not host-specific—it is associated with large, widely distributed, oceanic species of needlefishes.

The contrast is sharp among *Ablennes*, *Tylosurus acus*, and *T. crocodilus*, which are commonly infested with *Lernanthropus tylosuri*, and most of the species of *Strongylura*, which are usually infested with *L. belones*, particularly in the western Atlantic and eastern Pacific. The situation is confused in the Indo-West Pacific where nearly half of the *S. anastomella* examined were infested with *L. tylosuri*, and several other species of *Strongylura* have *L. belones*, or *L. tylosuri*, or both. *S. strongylura* has about an equal percentage of infestation of both species of *Lernanthropus*. The common character of *L. tylosuri* hosts is avoidance of estuarine areas. Most of the hosts are large offshore species as is true of *Caligodes* hosts. The common character of *L. belones* hosts is its likelihood of being taken in estuarine situations. We conclude that the reason for host differences between *L. belones* and *L. tylosuri* is that *L. belones* is euryhaline and *L. tylosuri* stenohaline.

Bomolochid copepods associated with needlefishes are apparently not host specific. Tables 4 and 5 show *Parabomolochus bellones* common on all seven species in four genera in the western Atlantic, on five of seven species in five genera in the eastern Atlantic, and on seven species of *Lhotskia* and *Strongylura* in the Indo-West Pacific. *P. bel-*

TABLE 5.—*Percentage of specimens of 16 marine species of needlefishes infested by 10 species of copepods*

Area, species, and number of specimens	*Parabomolochus*			*Nothobomolochus*	*Caligodes laciniatus*	*Lernanthropus*		*Colobomatus goodingi*	*Caligus* spp.
	bellones	*constrictus*	*ensiculus*	*gibber digitatus*		*tylosuri*	*belones*		
	Percent								
West Atlantic:									
S. marina (126)	42					2	29	5	
S. notata (200)	25						25	21	1
S. timucu (263)	30					.4	27	10	
East Atlantic:									
B. belone (77)	27			1					1
B. svetovidovi (15)	7			20					
S. senegalensis (27)	19								
Indo-West Pacific:									
L. gavialoides (24)	33				29	6			
S. anastomella (33)	42					45	3		3
S. leiura (49)	2			8	10	6			
S. incisa (67)	3					1	10		4
S. strongylura (59)	3			20		10	15		
S. urvillii (18)	6					6			6
T. choram (18)					22	6			6
T. punctulatus (31)				6		6	10		
East Pacific:									
S. exilis (97)		9	13			4	14	1	1
S. scapularis (31)		23	68				13		

lones is replaced by a derivative species in the eastern Pacific—*P. constrictus*. This copepod is abundant on all six eastern Pacific needlefishes and has also been found on four other species of inshore fishes in two different families. These two copepods seem to be found on whatever needlefish is available and may also occur on non-needlefish hosts.

Host-Parasite Distribution

To summarize the known distributions of needlefishes and their copepods and to contrast the distribution of a given species of needlefish with its associated copepods, 12 maps were prepared. Six maps (figs. 175–180) were made for the needlefishes: one for each of the four worldwide species (*Ablennes hians*, *Platybelone argalus*, *Tylosurus acus*, and *T. crocodilus*); one for the 11 marine species of *Strongylura;* and one for the fresh-water species of needlefishes and fresh-water populations of primarily marine species of *Strongylura*. Six maps (figs. 181–186) of copepod distributions were also made: *Caligodes laciniatus; Colobomatus goodingi; Lernanthropus belones* and *L. tylosuri;* the four species of *Parabomolochus; Nothobomolochus gibber* and *N. digitatus;* and the nine species of Ergasilidae. The needlefish maps are based on all of the specimens of needlefishes examined by Collette for his revisionary studies. The copepod maps are based on all of the copepods collected for this study. Not all of the needlefishes were examined for copepods so the needlefish maps have greater coverage than the copepod maps. Less abundant species of both needlefishes and copepods were not mapped. The 75° F. (23.9° C.) or 80° F. (26.7° C.) sea surface isotheres from Hutchins and Scharff (1947) are plotted on the 10 maps of marine species. These isotheres delimit the ranges remarkably well except along part of the mainland coasts where inshore species of *Strongylura* can move beyond the limits of the isothere.

In general, copepod distributions correspond to needlefish distributions. Most of the widely distributed species extend as far north and south as their hosts. There is, however, one striking exception: *Colobomatus goodingi* is restricted to warmer waters than its hosts—80° F. (26.7° C.) rather than 75° F. (23.9° C.) isotheres (Hutchins and Scharff, 1947). This difference is clearest in the western Atlantic where *Colobomatus* is confined to the region of the Gulf of Mexico and Caribbean Sea (lat. 10–30° N.—fig. 182). Although one of its primary hosts, *Strongylura notata* (fig. 179), has a similar restriction, other major hosts such as *S. marina*, *S. timucu*, and *T. crocodilus* (figs. 178, 179) range much farther to the north (past lat. 40° N.) and south (past lat. 20° S.).

Lernanthropus belones has an apparent gap in distribution (fig. 183). Both *L. belones* and *L. tylosuri* seem to be equally common throughout the world except for the eastern Atlantic and western Indian Oceans where we have found only *L. tylosuri*. We believe this break is primarily due to the lack of proper hosts for *L. belones* in these *Strongylura*-deficient regions. The eastern Atlan-

tic has only one species of *Strongylura*—*S. senegalensis*—and it is confined to the Gulf of Guinea. The western Indian Ocean has only one *Strongylura*—*S. leiura*—a large offshore species infested (rarely) with *L. tylosuri* and apparently never with *L. belones*. *L. belones* probably will be found to occur on *S. senegalensis*, so part of the distributional gap will be filled in. There does, however, appear to be a real gap in the distribution of *L. belones* that tends to divide the worldwide population. Perhaps detailed analysis of geographic variation in *L. belones* will provide morphological support for this geographical two-population hypothesis. The ovigerous females from the Atlantic and the Indo-West Pacific show a difference in total length (See discussion of intraspecific variation in copepods and fig. 187).

As has been noted previously, the widespread *Parabomolochus bellones* is replaced by two species in the eastern Pacific—the closely related *P. constrictus* and the more distantly related *P. ensiculus* (fig. 184). The Eastern Pacific Barrier, so important in blocking the distribution of shore fishes (Briggs, 1961), seems to operate as effectively within this genus of needlefish copepods.

Parabomolochus bellones appears to be in the process of being replaced in the eastern Indian and western Pacific Oceans by *P. sinensis* and the two species of *Nothobomolochus*. This replacement is partially apparent from a comparison of the distribution of *Parabomolochus* (fig. 184) with *Nothobomolochus* (fig. 185). In the western Pacific, *P. bellones* is common in Japan and Australia, between the 75° and 80° F. isotheres (23.9° C. and 26.7° C.—Hutchins and Scharff, 1947), whereas the other three bomolochids are common in the tropical waters. Relative abundance of *P. bellones* also differs from that of the other bomolochids (tables 4 and 5). *P. bellones* is very abundant in the western Atlantic (infestations ranging up to 42 percent). It is also equally abundant on most hosts in the Gulf of Guinea and Mediterranean Sea. However, *N. gibber* has largely replaced *P. bellones* on one host—*Belone svetovidovi*. In the Indo-West Pacific, *P. sinensis* and the two species of *Nothobomolochus* replace *P. bellones* on some hosts, particularly *Ablennes hians* and *Platybelone argalus* in the western and southern Pacific. Perhaps *P. sinensis* and the two species of *Nothobomolochus* evolved more recently and have begun to replace the older *Parabomolochus bellones* in the warmer parts of the Indo-West Pacific oceans.

The distributional maps of ergasilid copepods (fig. 186) and their fresh-water needlefish hosts (fig. 180) may also be compared. With one exception, the ranges of the host species are greater than those of their ergasilid copepods. The exception is the presence of what we have called *Ergasilus orientalis* on *Potamorrhaphis* in the Amazon Basin and on *Strongylura incisa* from Arnhem Land, Australia. We do not believe that this is a widespread species, but Cressey has been unable to discover any significant differences between the two populations; for the present we let this distributional pattern stand.

Probably the most widely distributed ergasilid copepod considered here is *Ergasilus coleus*. This copepod has been collected on three different hosts: the fresh-water *Xenentodon cancila* from India; the estuarine *Strongylura strongylura* from India, Borneo, and the Philippine Islands; and the primarily marine *S. urvillii* from the Philippines. This extensive distribution argues for either a greater degree of salt tolerance than is usually found in ergasilids or an old distributional pattern dating back to when the fresh waters of southeast Asia, Borneo, and the Philippines were connected, permitting the transfer of fresh-water fishes and their parasites.

Intraspecific Variation in Copepods

Studies were made of the variation in total length in *Caligodes laciniatus* and *Lernanthropus belones* and in relative lengths of two setae on leg 5 of *Parabomolochus bellones*.

As discussed under *Caligodes*, the total length of ovigerous females of this copepod varies widely. We analyzed this variation by host and by area (table 2). By area, the ranges and mean lengths were: Atlantic 2.4 to 7.1 (4.36), Indo-West Pacific 2.5 to 5.6 (3.70), and eastern Pacific 3.4 to 6.6 (4.29). By hosts, *Ablennes hians* stands out with by far the largest *Caligodes* 5.3 to 7.1 (6.03) compared to five other host species 2.4 to 5.6 (means 3.77–4.66). Although evidence is clear for differences in lengths of copepods by host species and not by geographic areas; we do not know if the host directly influences the growth of the copepod or whether the host's environment does so.

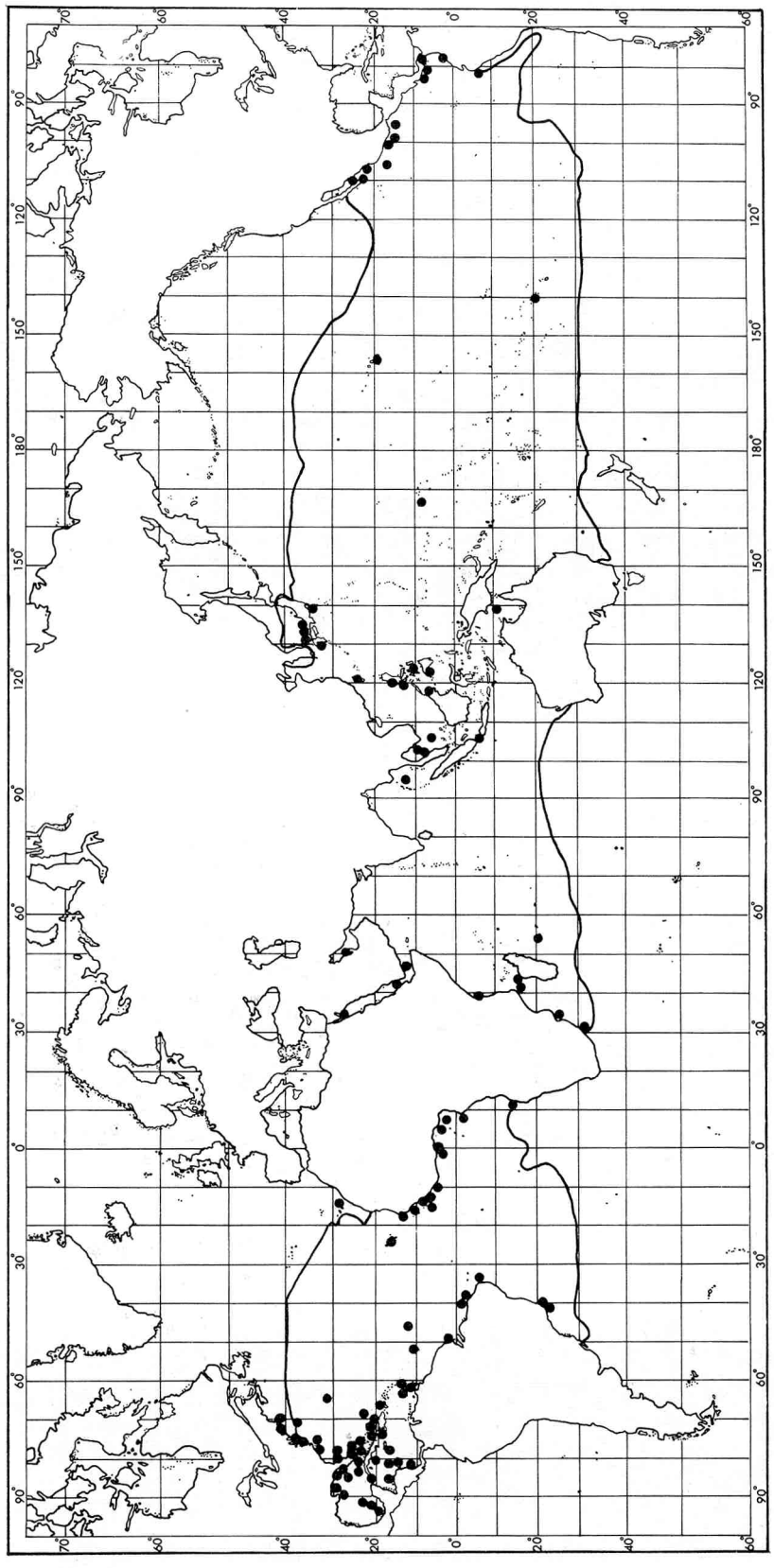


FIGURE 175.—Distribution of *Ablennes hians* based on specimens examined in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

373-320 O—70——9

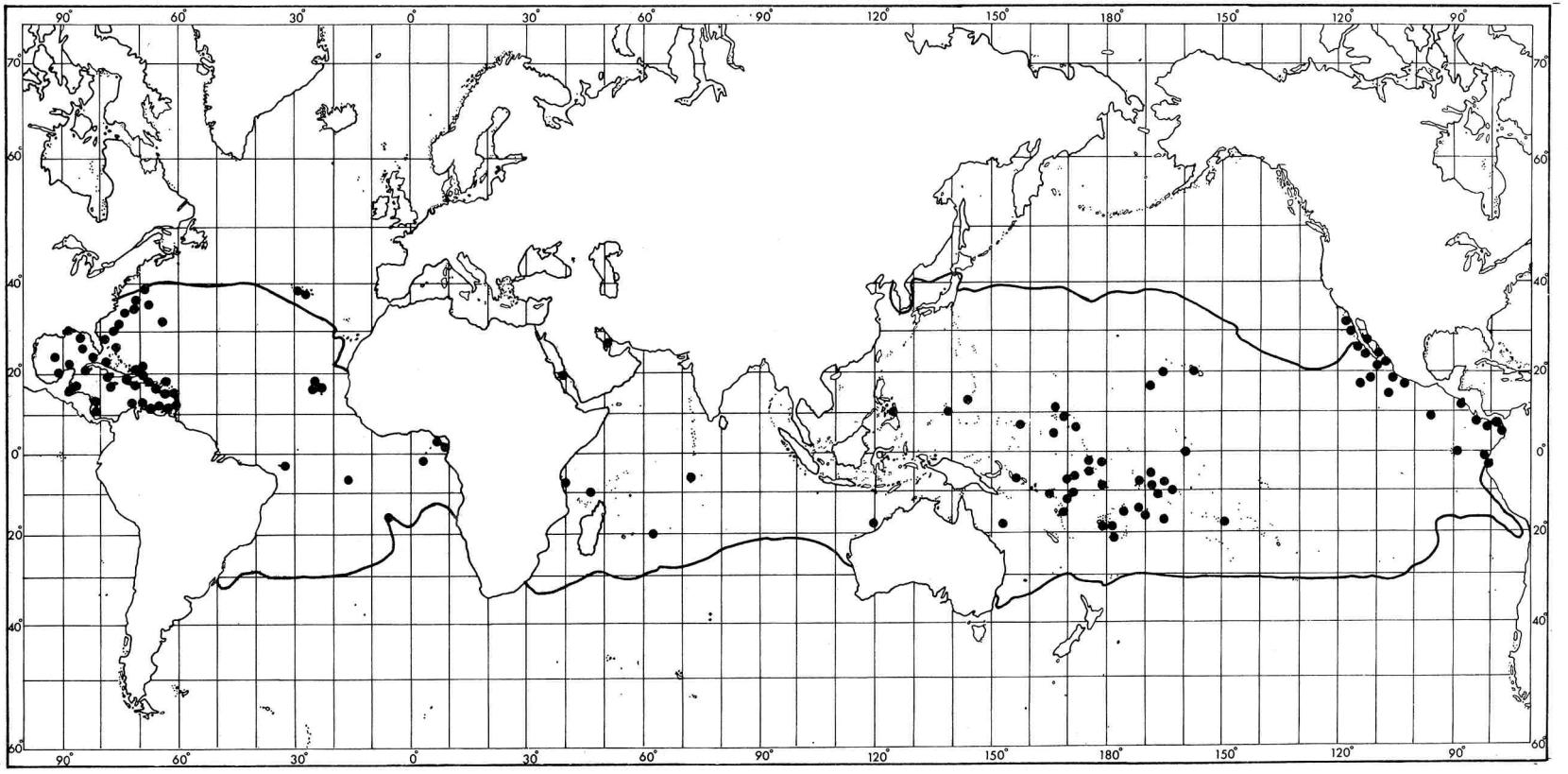


FIGURE 176.—Distribution of *Platybelone argalus* based on specimens examined in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

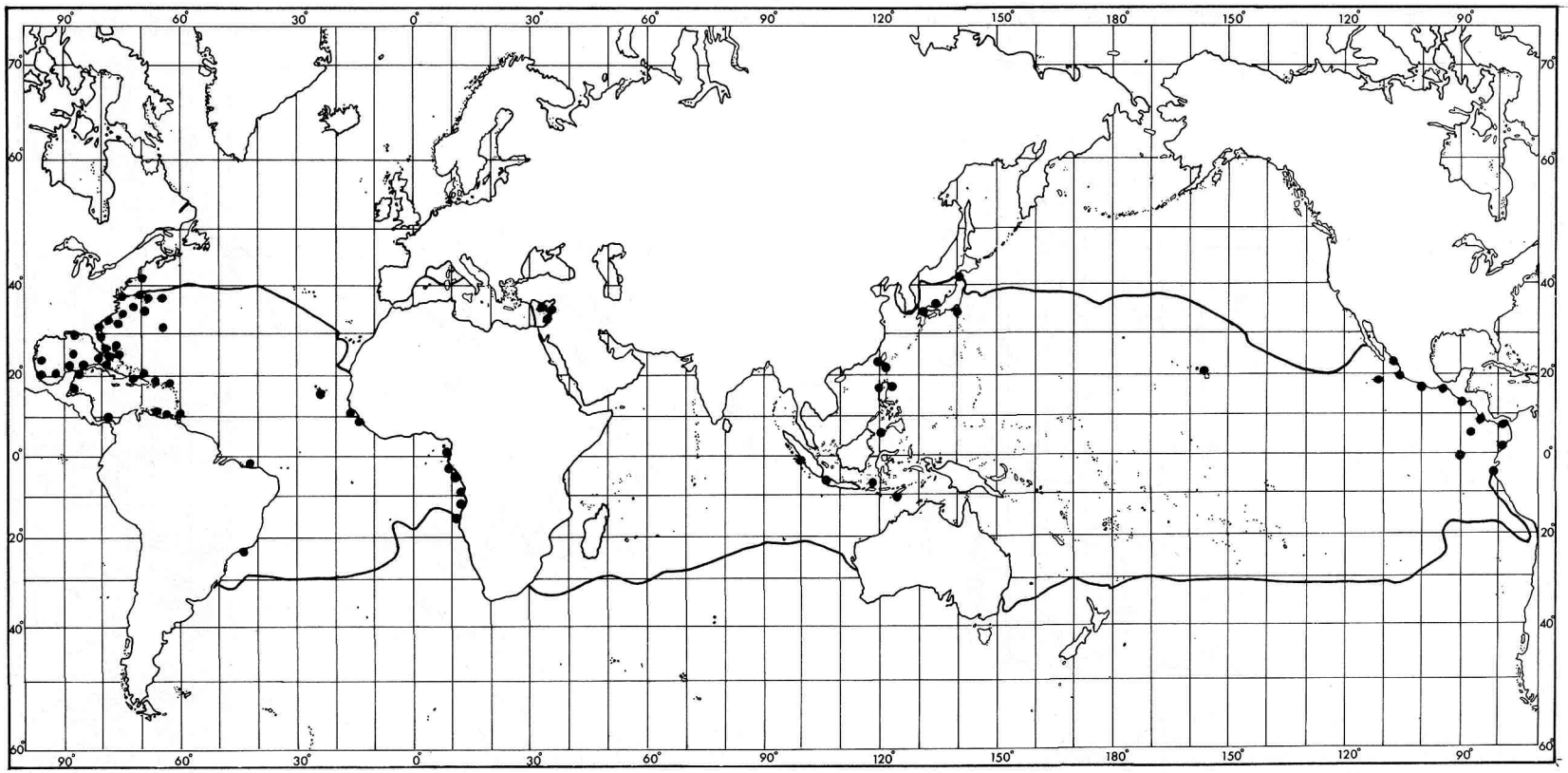


FIGURE 177.—Distribution of *Tylosurus acus* based on specimens examined in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

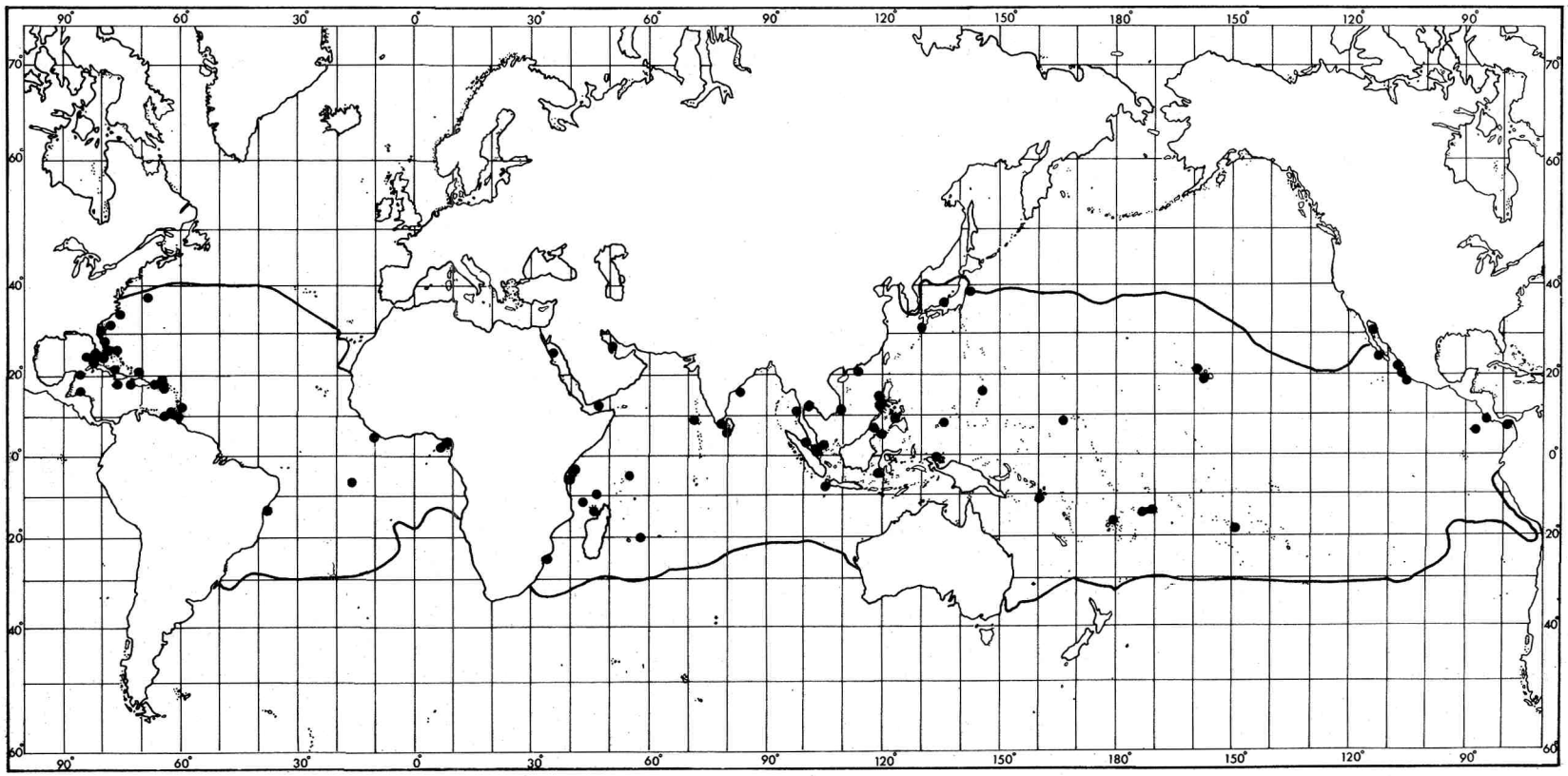


FIGURE 178.—Distribution of *Tylosurus crocodilus* based on specimens examined in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

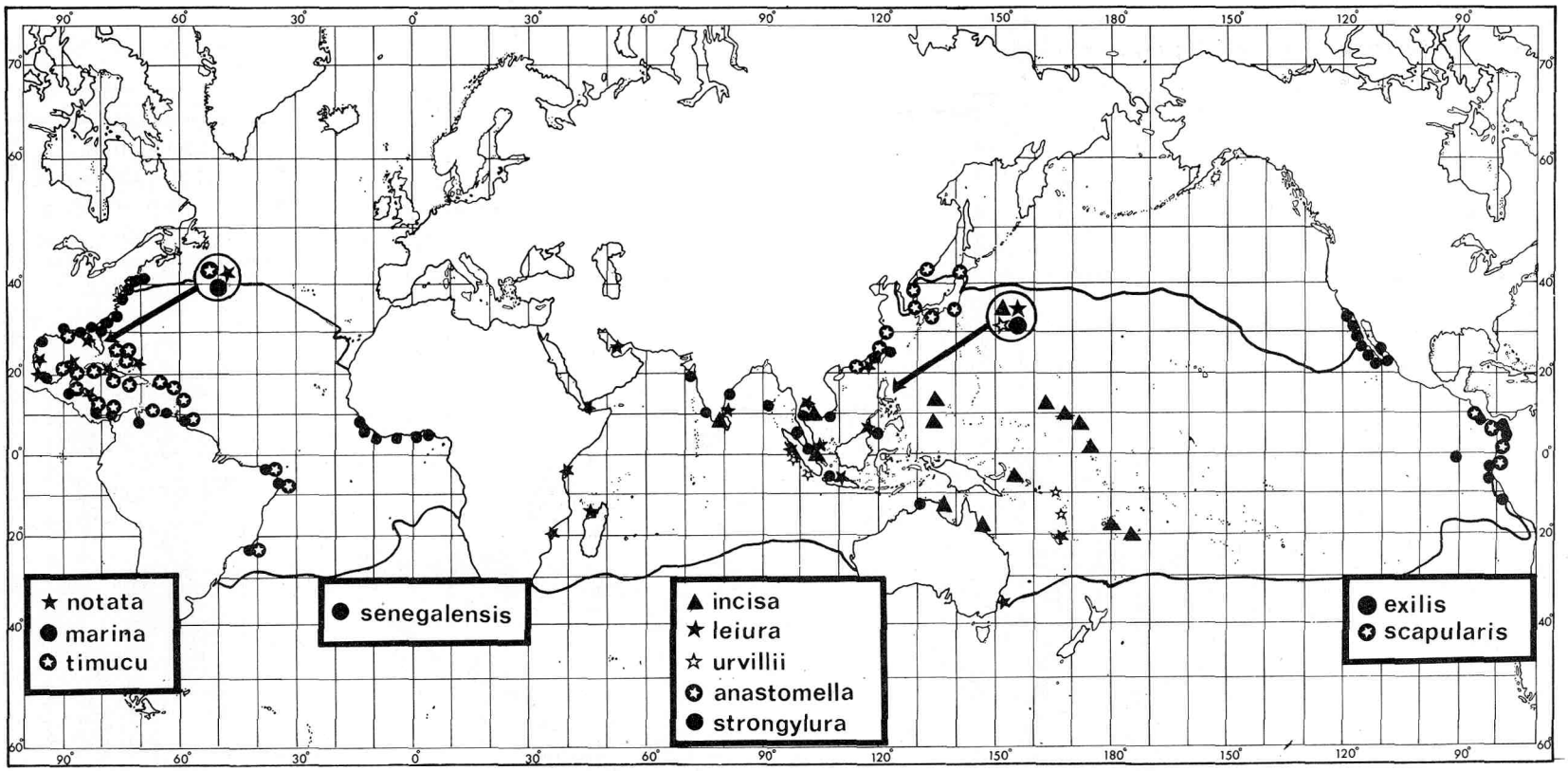


FIGURE 179.—Distribution of marine populations of 11 species of *Strongylura* based on specimens examined in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

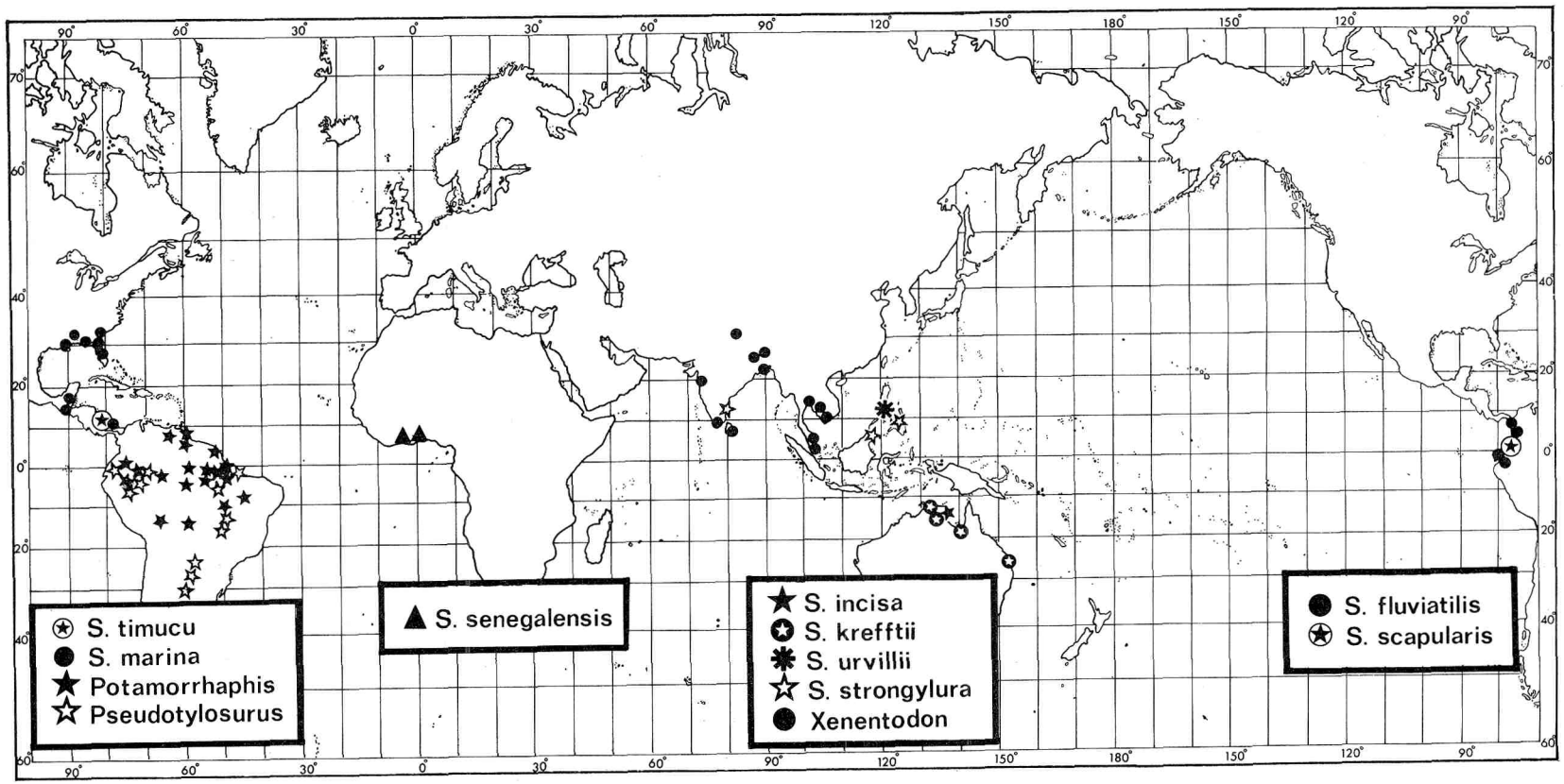


FIGURE 180.—Distribution of fresh-water needlefishes including fresh-water populations of *Strongylura* based on specimens examined.

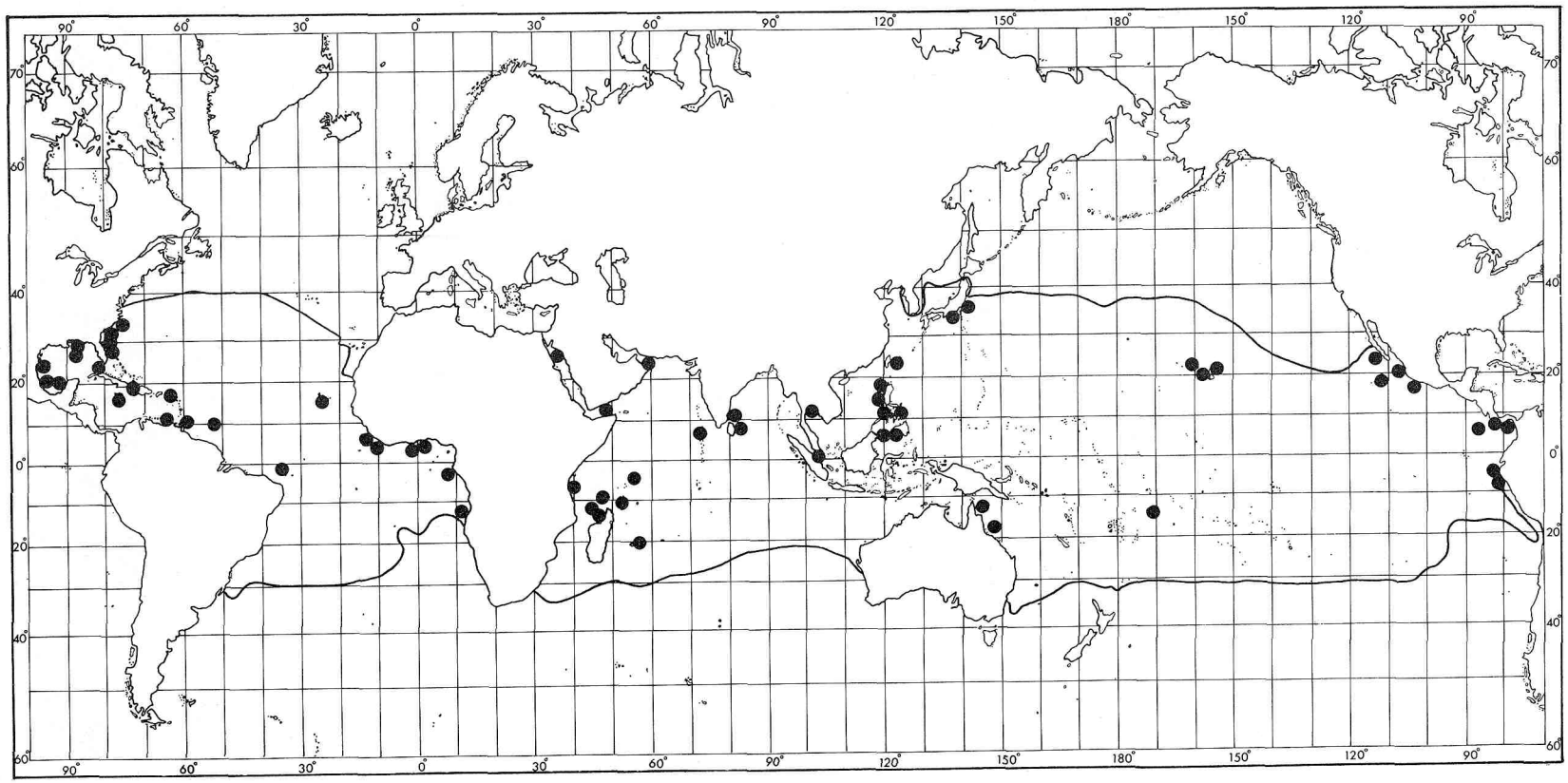


FIGURE 181.—Distribution of *Caligodes laciniatus* from needlefishes in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

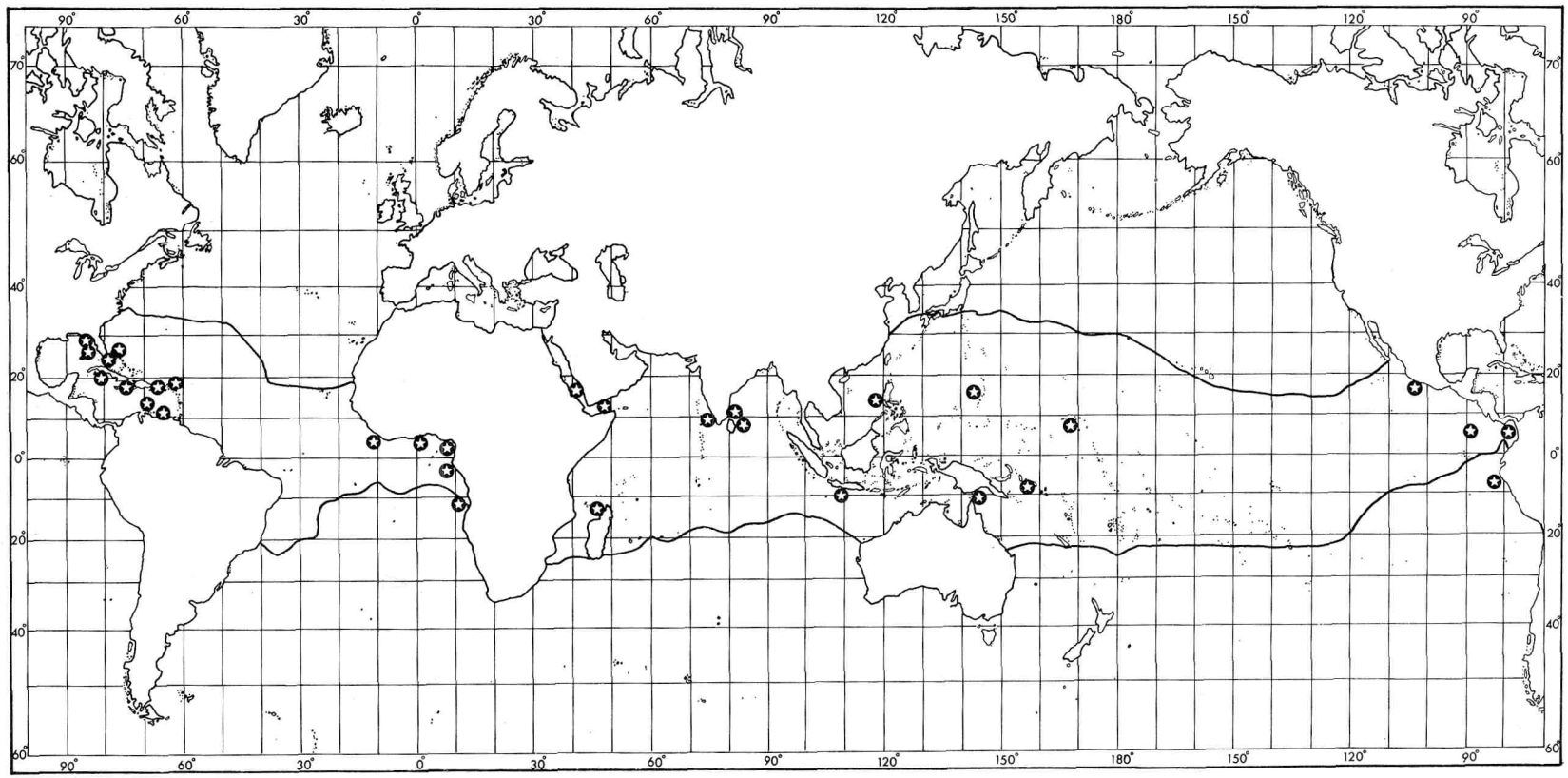


FIGURE 182.—Distribution of *Colobomatus goodingi* from needlefishes in relation to the 80° F. (26.7° C.) isothere from Hutchins and Scharff (1947).

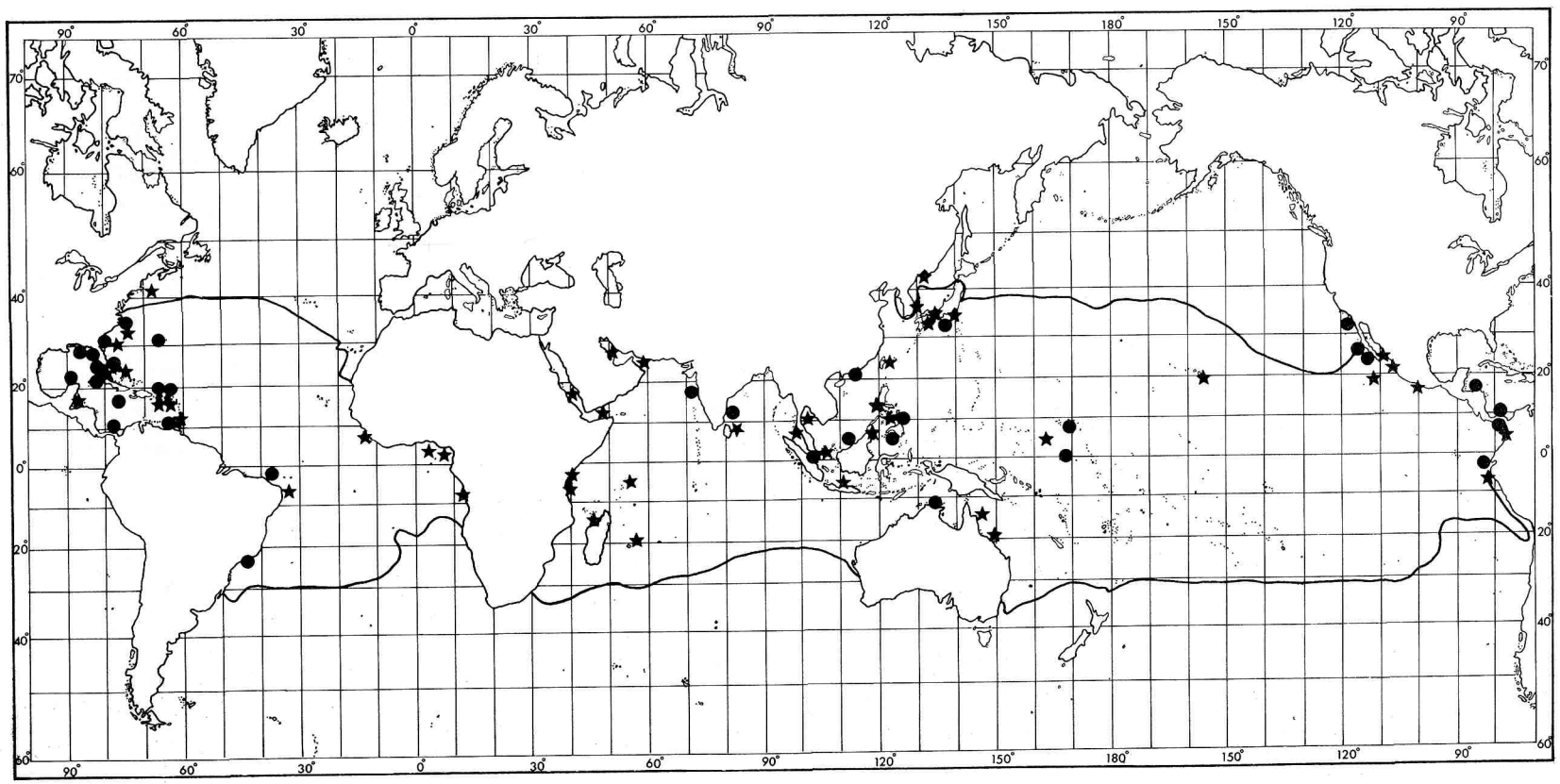


FIGURE 183.—Distribution of *Lernanthropus belones* (dots) and *L. tylosuri* (stars) from needlefishes in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

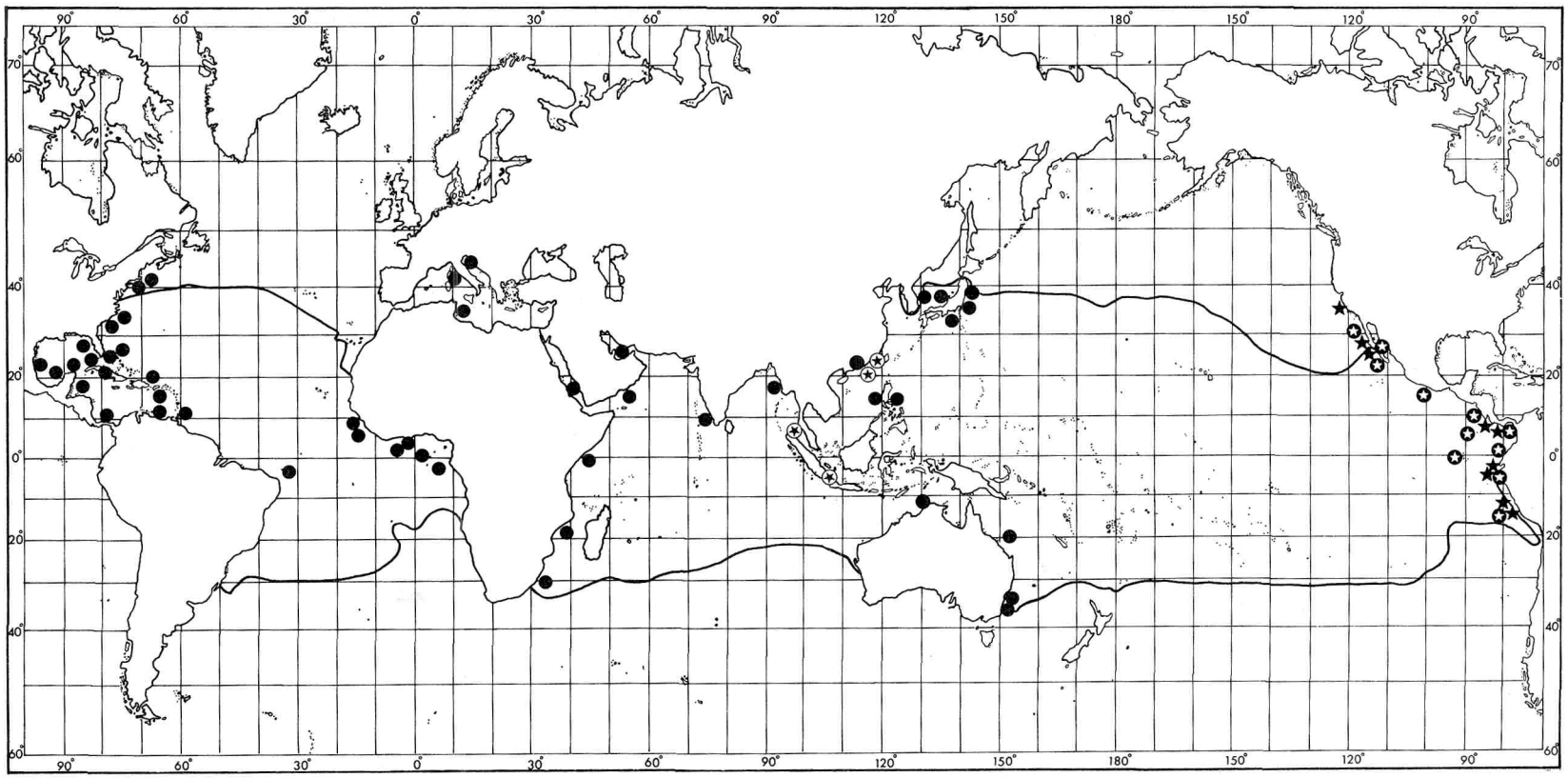


FIGURE 184.—Distribution of four species of *Parabomolochus* from needlefishes in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947). Dots—*P. bellones*, stars—*P. ensiculus*, stars in circles—*P. sinensis*, white stars (eastern Pacific)—*P. constrictus*.

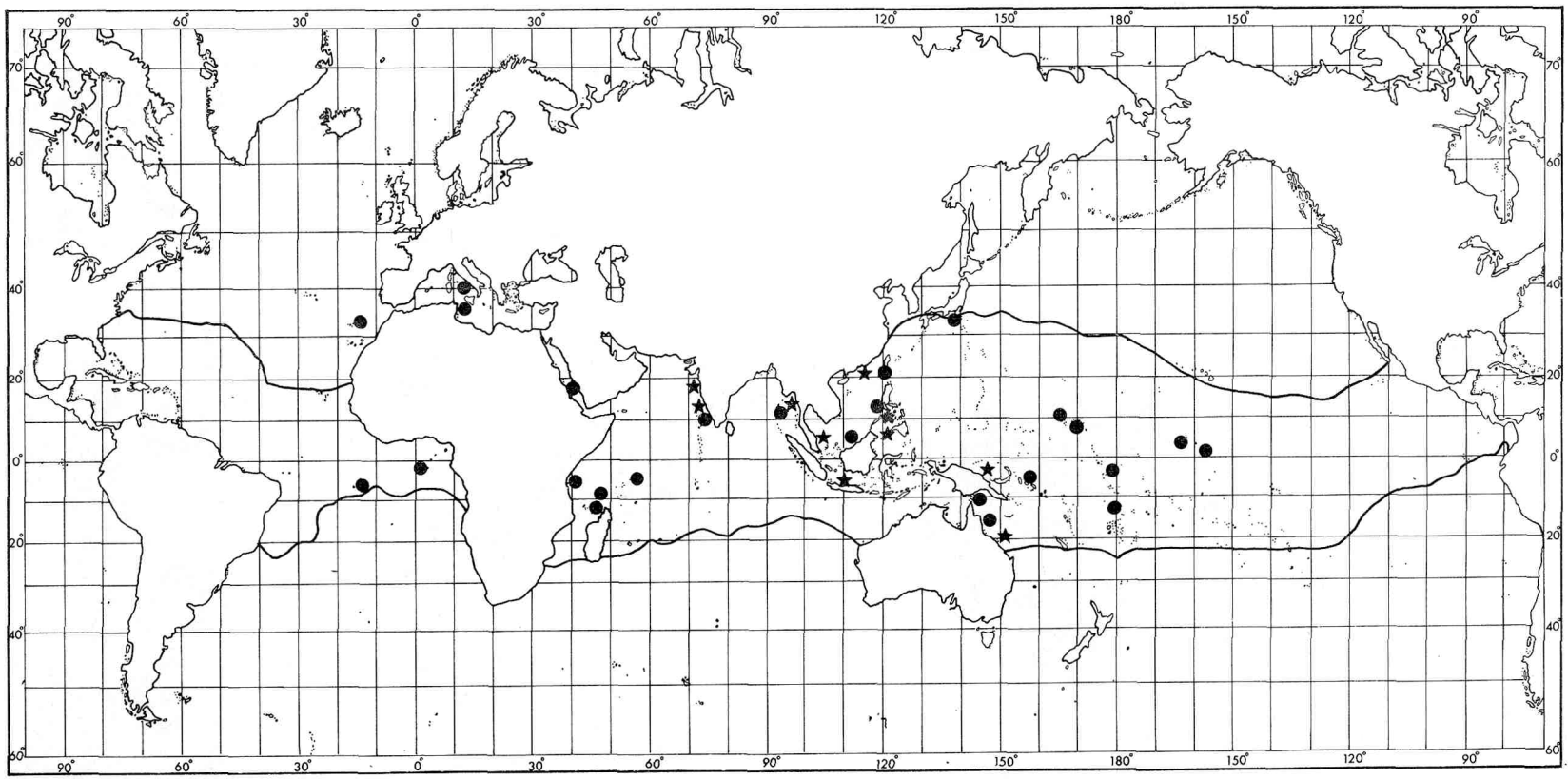


FIGURE 185.—Distribution of *Nothobomolochus gibber* (dots) and *N. digitatus* (stars) from needlefishes in relation to the 80° F. (26.7° C.) isothere from Hutchins and Scharff (1947).

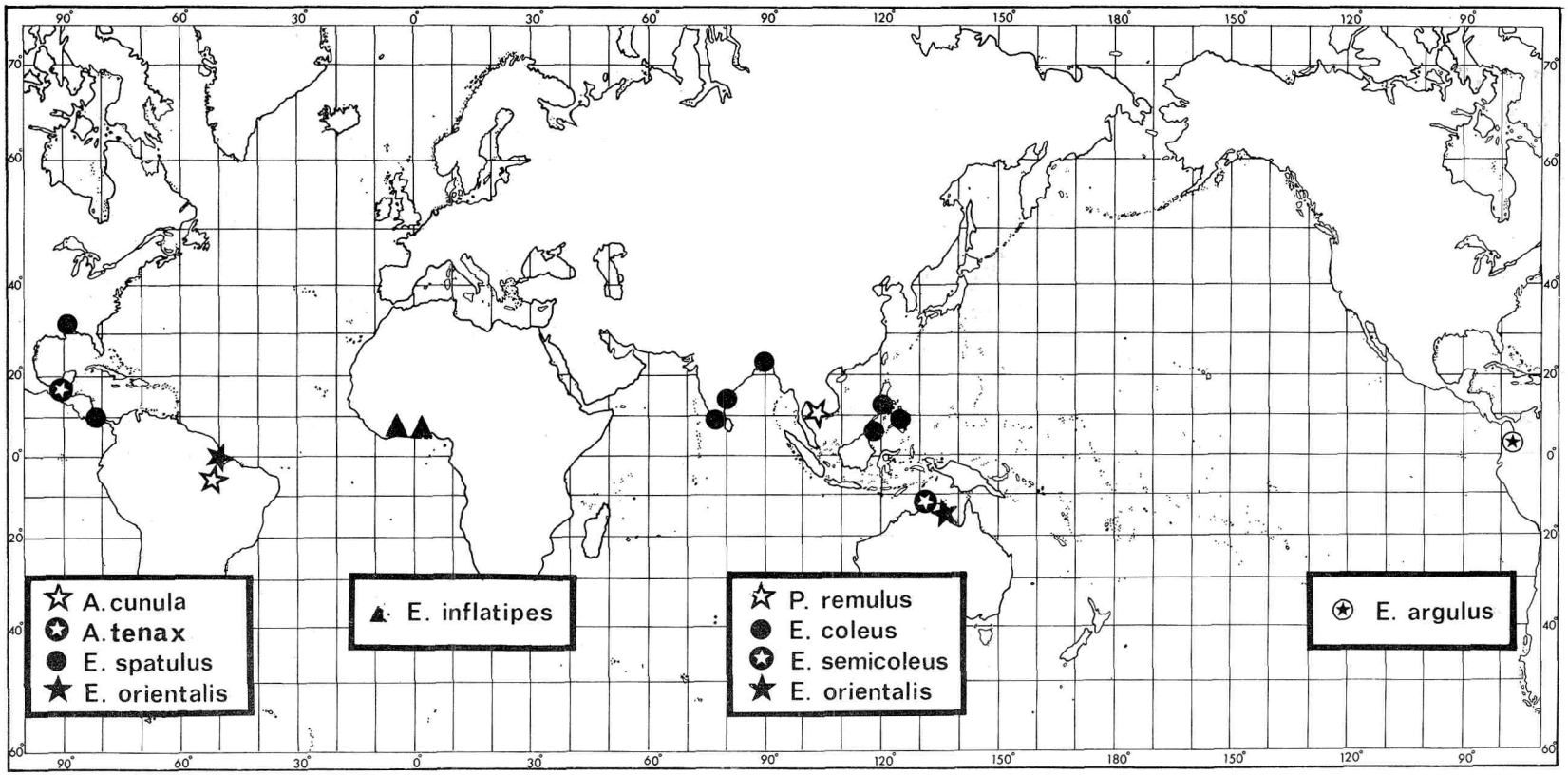


FIGURE 186.—Distribution of ergasilid copepods of the genera *Acusicola*, *Ergasilus*, and *Paraergasilus* from needlefishes.

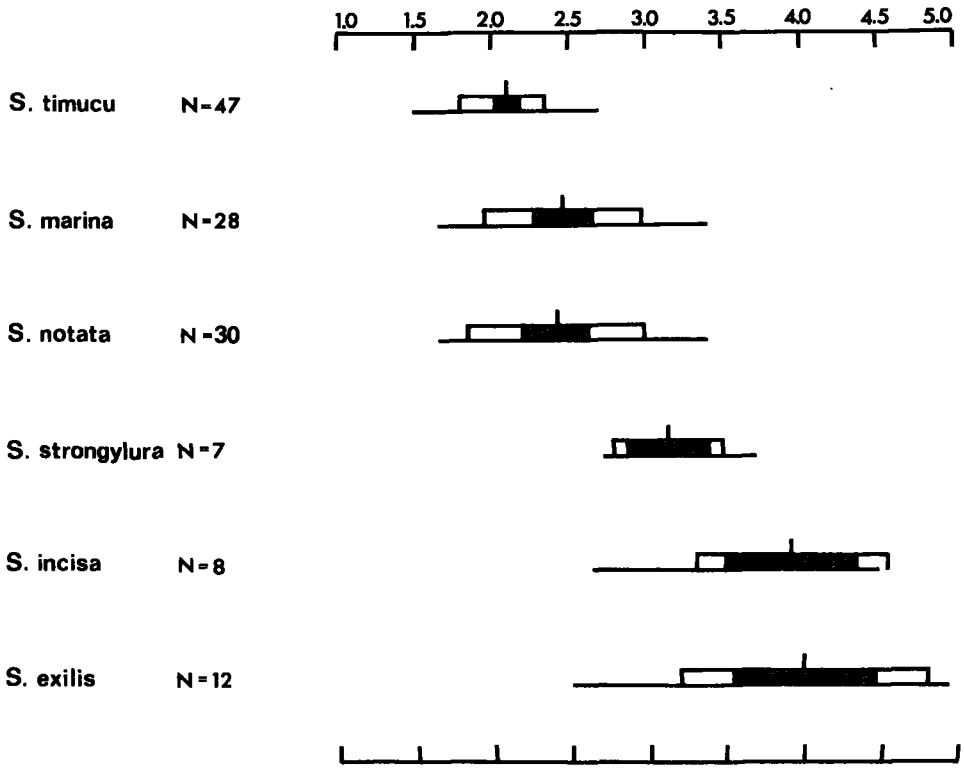


FIGURE 187.—Total length (in μ) of ovigerous female *Lernanthropus belones* from six species of *Strongylura* arranged from W. Atlantic east to E. Pacific. The horizontal line represents the range, the vertical line the mean, the filled-in rectangle two standard errors on each side of mean, and open rectangle one standard deviation on each side of mean.

The total length of ovigerous female *Lernanthropus belones* also varies: copepods from the three western Atlantic hosts are significantly smaller than those from the two Pacific hosts (fig. 187). *Strongylura strongylura* is geographically intermediate (Indo-West Pacific) and has intermediate-sized *L. belones*. The Pacific hosts (*S. incisa* and *S. exilis*) do reach a greater length than the other four species of hosts, but the possible host-parasite size correlation breaks down: *S. strongylura*, the smallest of the six host species, does not have the smallest copepods.

The relative lengths of the two setae on leg 5 in *Parabomolochus* have been examined by area (fig. 188) and by host (fig. 189). The first set of Hubbs-Perlmutter diagrams in each figure is of a sample of 50 *P. bellones* taken from one collection of *Strongylura notata* at Sarasota, Fla. This diagram gives a measure of the amount of variation to be expected in setae lengths of a single population from one host species at one time and place. The smaller ratio of seta 1 to 2 distinguishes the eastern Pacific *P. constrictus* from its probable ancestor *P. bellones*. The higher ratio distinguishes *P. sinensis* from either of these. The difference in the ratio is primarily due to the much greater length of seta 2 in *P. constrictus* and the shorter length of seta 2 coupled with a longer seta 1 in *P. sinensis*. Neither the absolute lengths of seta 1 and seta 2 nor their ratio varies significantly among the populations living on the three hosts of *P. constrictus* in the eastern Pacific Ocean. Variation is extensive, however, among populations of *P. bellones*. The populations in the five subareas of the western Atlantic all have similar absolute lengths of both setae, and their ratios are nearly identical. The Gulf of Guinea and Mediterranean populations have seta 1 somewhat longer, resulting in a significantly higher ratio of seta 1 to seta 2. Setae lengths differ among three western Pacific populations—Japan, Australia, and Philippines—but their ratios are nearly identical.

Thus, in *Caligodes laciniatus* at least, intraspecific variation in the copepod is related to host

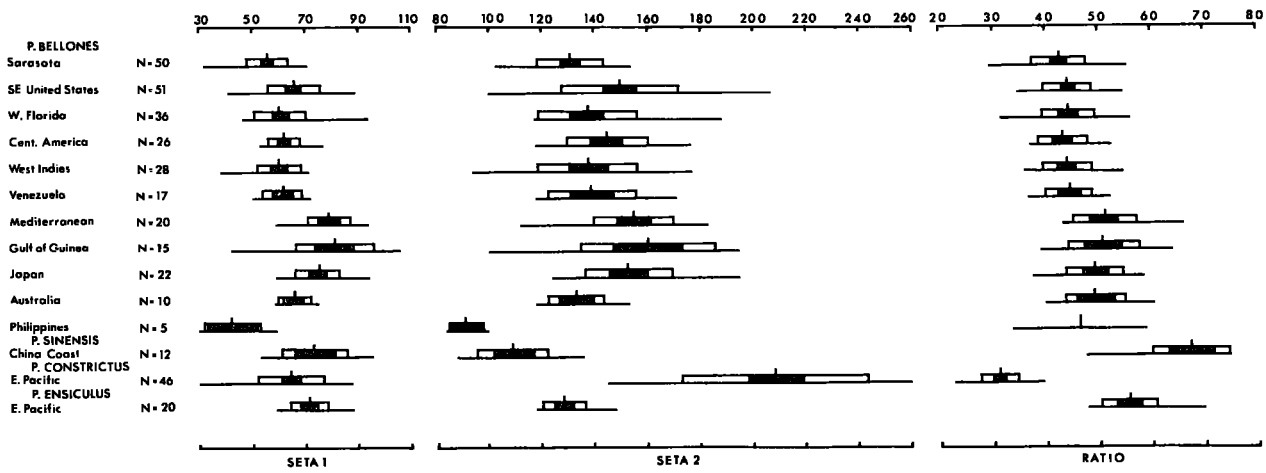


FIGURE 188.—Lengths of two setae on leg 5 of four species of *Parabomolochus* by geographic area. Symbols as in figure 187. The first line represents a single sample from *Strongylura timucu* from Sarasota, Fla.

influence or the ecology of the host. And in *Lernanthropus belones* and *Parabomolochus bellones*, intraspecific variation is clearly geographic.

Relative Rates of Evolution

An often cited axiom of modern parasitology asserts that because parasites evolve more slowly than their hosts, information on the parasites will assist in understanding the evolution of the hosts. In other words, hosts that harbor closely related parasites may themselves be closely related. This axiom is related to the question of host specificity. Four worldwide species of copepods (*Caligodes laciniatus*, *Lernanthropus belones*, *L. tylosuri*, and *Colobomatus goodingi*) show little geographic variation except in total length. The four worldwide species of needlefishes show varying amounts of geographic variation (Collette and Parin, 1970). This variation is weakest in *Ablennes hians*. *Tylosurus crocodilus* has at least two subspecies, one restricted to the eastern Pacific. *T. acus* has five subspecies: western Atlantic, Mediterranean, Gulf of Guinea, Indo-West Pacific, and eastern Pacific. *Platybelone argalus* has seven subspecies: western Atlantic, Annobon-Fernando Póo, Ascension-St. Helena, Cape Verdes, Red Sea, Indo-West Pacific, and eastern Pacific. Thus, the four worldwide species of needlefishes appear to be more highly differentiated than are the four worldwide species of copepods. It must be remembered, though, that studies of geographic variation have not been carried out in copepods with the same degree of thoroughness as in fishes.

Another widespread copepod, *Parabomolochus bellones*, has differentiated to the specific level (*P. constrictus*) after isolation in the eastern Pacific. In comparison, three of the four worldwide hosts have differentiated to only the subspecific level. Here, evolution may have proceeded faster in the copepod than in its host. The apparent "loose" specificity to their hosts of the cyclopoid copepods discussed here may explain the unsettled nature of their relationship.

Effect of Host Size

Another parasitological axiom states that older (=larger) host individuals have a greater parasite fauna because they have been exposed longer. To examine this axiom, data were examined on the mean body lengths of the commonest 16 species of marine needlefishes infested with the commonest 8 species of copepods. The copepods were divided into two major categories: specialized (*Lernanthropus*, *Caligodes*, *Colobomatus*) and generalized (*Parabomolochus* and *Nothobomolochus*). By specialized we mean possessing adaptations used as holdfasts (and exhibiting a higher degree of host specificity); by generalized we mean those copepods (Bomolochidae) that are free to wander about (and show less host specificity). Because the species of needlefishes vary widely in length, a ranking comparison was used to substitute relative

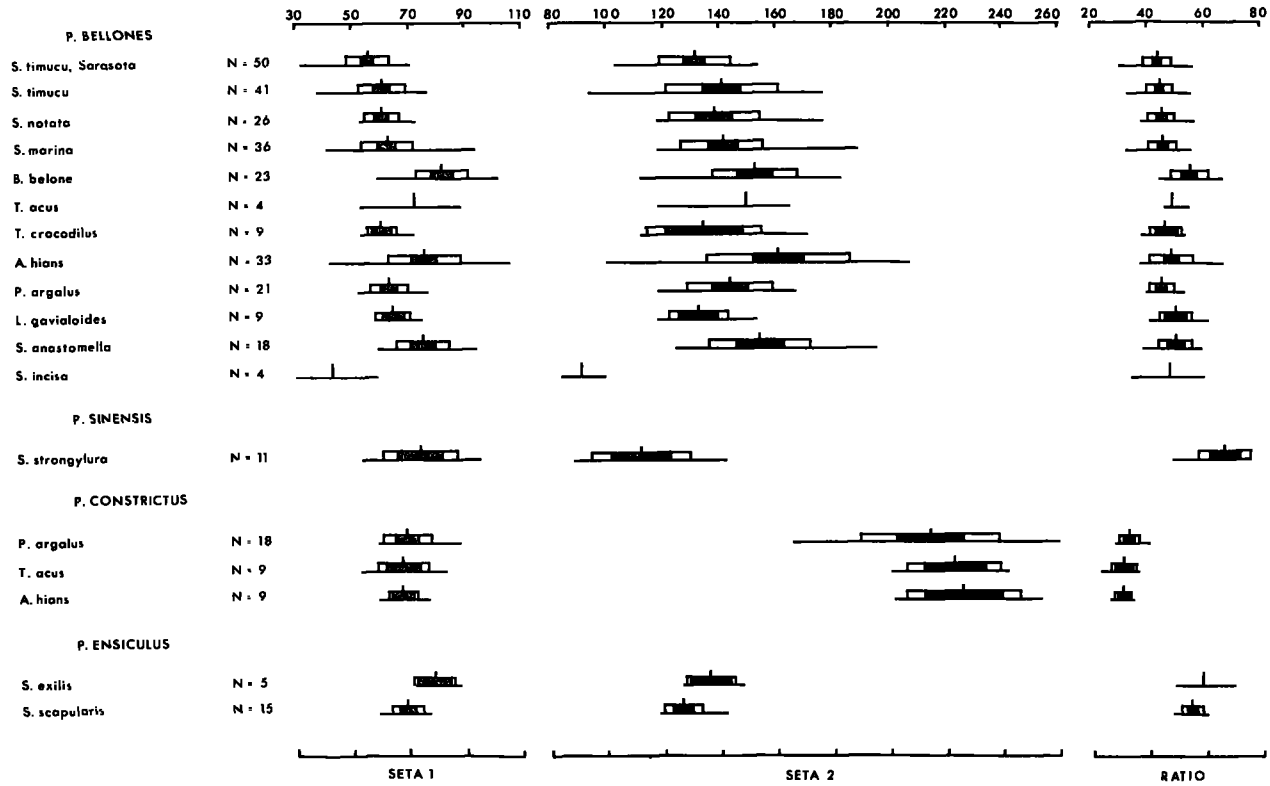


FIGURE 189.—Lengths of two setae on leg 5 of the species of *Parabomolochus* by hosts. Symbols as in figure 187.

length for absolute length. For each species of needlefish infested with a given species of copepod, three mean body lengths were compared: mean body length of all specimens examined, mean body length of all specimens that lacked copepods, and mean body length of all specimens infested with the particular copepod. The least mean body length was ranked 1, the next 2, and the greatest 3.

The specialized copepods (table 6) show consistent results. Without exception, the needlefishes without a specific copepod had the smallest mean body length (1) and the needlefishes with a particular species of specialized copepod had the largest mean body length (3). The mean body length of the total specimens examined was intermediate (2). We interpret this sequence to mean that these four specialized species of copepods are attached to needlefishes of larger than average size because of needing sufficient space and time to become attached.

The generalized copepods show a different picture. As with the specialized copepods, three species (*Parabomolochus constrictus*, *P. ensiculus*, and *Nothobomolochus gibber*) are usually found on needlefishes with greater mean body lengths than the needlefishes with no copepods. Summing the ranks for each of these three species of copepods, however, shows that the mean body lengths of needlefish infested with one of these copepods is about equal to the mean body lengths of the total number of needlefishes examined. Thus, the distribution of these three copepods is unrelated to the size of the needlefishes.

Unlike the situation with the seven species of copepods previously discussed, the mean body length of specimens infested with *Parabomolochus bellones* is equal to or less than the mean body lengths of all specimens examined. This fact seems to indicate that *P. bellones* selects smaller specimens of needlefishes to infest.

The above analysis confirms the subjective impressions that Collette gained while collecting copepods from preserved needlefishes: bomolochids more frequently infest smaller needlefishes than do the specialized copepods. Also, the chance of finding an individual needlefish infested with one

TABLE 6.—*Ranking comparisons of mean body lengths of all specimens of needlefish species examined with mean body lengths of specimens with no copepods and specimens with a particular copepod (1=smallest mean body length; 3=largest mean body length)*

Needlefishes with generalized copepods				Needlefishes with specialized copepods			
Needlefish species	All specimens	No copepods	*Parabomolochus bellones*	Needlefish species	All specimens	No copepods	*Lernanthropus belones*
Ablennes hians	3	1	2	*Strongylura exilis*	2	1	3
Belone belone	2	3	1	*Strongylura marina*	2	1	3
Platybelone argalus	3	2	1	*Strongylura notata*	2	1	3
Lhotskia gavialoides	2	3	1	*Strongylura scapularis*	2	1	3
Strongylura anastomella	2	1	3	*Strongylura strongylura*	2	1	3
Strongylura marina	3	2	1	*Strongylura timucu*	2	1	3
Strongylura notata	3	1	2	Total	12	6	18
Strongylura timucu	2	1	3				
Tylosurus acus	3	2	1				*Lernanthropus tylosuri*
Tylosurus crocodilus	3	2	1	*Ablennes hians*	2	1	3
Total	26	18	16	*Strongylura anastomella*	2	1	3
			Parabomolochus constrictus	*Strongylura leiura*	2	1	3
Ablennes hians	3	1	2	*Strongylura strongylura*	2	1	3
Platybelone argalus	2	1	3	*Tylosurus acus*	2	1	3
Strongylura exilis	2	1	3	*Tylosurus crocodilus*	2	1	3
Strongylura scapularis	3	1	2	Total	12	6	18
Tylosurus acus	3	1	2				
Tylosurus crocodilus	2	3	1				*Caligodes laciniatus*
Total	15	8	13	*Ablennes hians*	2	1	3
			Parabomolochus ensiculus	*Lhotskia gavialoides*	2	1	3
Strongylura exilis	3	1	2	*Tylosurus acus*	2	1	3
Strongylura scapularis	2	1	3	*Tylosurus crocodilus*	2	1	3
Total	5	2	5	Total	8	4	12
			Nothobomolochus gibber				*Colobomatus goodingi*
Ablennes hians	3	1	2	*Ablennes hians*	2	1	3
Platybelone argalus	1.5	1.5	3	*Strongylura marina*	2	1	3
Tylosurus crocodilus	3	2	1	*Strongylura notata*	2	1	3
Total	7.5	4.5	6	*Strongylura timucu*	2	1	3
				Tylosurus acus	2	1	3
				Tylosurus crocodilus	2	1	3
				Total	12	6	18

of the four specialized copepods increases greatly with the size of the needlefish.

Competition Between Copepods

Another question that we ask is: Does the presence of one species of copepod interfere with and thereby reduce the likelihood of infestation with a second species of copepod? We examined the relative numbers of individual needlefishes infested by more than one species of copepod (table 7) and then considered the combinations of copepod species (table 8) in the multiple-species infestations. Some individuals of half the species of needlefishes had two or more species of copepods. Most of these are either large species of needlefishes or species of which large numbers of specimens were examined. As shown in the previous section, the likelihood of infestation of a host by a specialized species of copepod increases with the size of the host. And obviously, the more specimens we examined, the more likely we were to find some individuals with more than one species of copepod.

The commonest combination of copepods (table 8) is *Parabomolochus bellones* and *Lernanthropus belones* (65 of 308 records). These combinations all come from the three western Atlantic species of *Strongylura*, *timucu* (33), *marina* (21), and *notata* (11), although both species of copepods occur from the western Atlantic through the western Pacific. The reason for the absence of this combination elsewhere is due to the lack of *L. belones* in the eastern Atlantic and western Indian Oceans which is caused by the scarcity of *Strongylura* hosts in these areas. Also, *P. bellones* is rarer in the Indian and Pacific Oceans where it is frequently replaced by *P. sinensis* and the two species of *Nothobomolochus*.

The next commonest combinations of copepods involve *Parabomolochus bellones*, *Colobomatus goodingi*, *Caligodes laciniatus*, and *Lernanthropus tylosuri*: *P. bellones* and *Colobomatus* (37 rec-

TABLE 7.—*Needlefish infestation by different numbers of copepod species as related to number of specimens examined and maximum host size (in mm. body length)*

Species	Species of copepods	Maximum BL	Total examined	Infested with copepods	With 2 species of copepods	With 3 to 5 species of copepods
	Number	*Mm.*	*Number*	*Percent*	*Percent*	*Percent*
Ablennes hians	8	725	251	57.0	10.8	3.2
Belone belone	3	537	77	44.2	0	0
Belone svetovidovi	2	320	15	26.7	0	0
Lhotskia gavialoides	2	665	24	54.2	8.3	0
Platybelone argalus	7	300	487	33.7	.2	0
Potamorrhaphis guianensis	1	157	63	3.5	0	0
Pseudotylosurus angusticeps	1	255	25	8.0	0	0
Strongylura anastomella	4	580	33	63.6	30.3	0
S. exilis	6	490	97	37.1	6.2	0
S. fluviatilis	1	321	33	12.1	0	0
S. incisa	5	450	75	17.3	0	0
S. krefftii	1	388	44	13.6	0	0
S. leiura	4	501	49	22.4	0	2.0
S. marina	7	418	316	32.0	7.0	0
S. notata	4	245	200	62.0	7.0	1.5
S. scapularis	4	245	38	84.2	15.8	0
S. senegalensis	2	263	27	81.5	0	0
S. strongylura	5	233	69	53.6	4.3	1.4
S. timucu	5	275	281	46.3	16.0	1.4
S. urvillii	4	228	21	19.0	0	0
Tylosurus acus	8	950	147	46.3	12.2	2.0
T. choram	3	415	18	33.3	0	0
T. crocodilus	8	860	212	56.6	18.9	3.8
T. punctulatus	3	385	31	22.6	0	0
Xenentodon cancila	2	169	65	15.4	0	0

ords); *Caligodes* and *L. tylosuri* (36); *P. bellones* and *L. tylosuri* (26); *L. tylosuri* and *Colobomatus* (25); and *Caligodes* and *Colobomatus* (22). The three species of needlefishes most involved in these combinations are the three large worldwide species: *Ablennes hians*, *Tylosurus acus*, and *T. crocodilus*. They account for almost all the *Caligodes–L. tylosuri*, *Caligodes–Colobomatus*, and *L. tylosuri–Colobomatus* combinations (76 of 83 records). *T. crocodilus* and *Ablennes* are also important in the *P. bellones–Colobomatus* and *P. bellones–L. tylosuri* combinations (27 records) but three species of *Strongylura* are also involved: *S. timucu* (16 records) and *S. notata* (6) in the former combination and *S. anastomella* (10) in the latter.

All the common combinations mentioned above (212 of 308 records) involve copepods living in different ecological niches on their host needlefishes: *Caligodes* under the oral valves, *Colobomatus* in the cephalic lateral line canals, *Lernanthropus* attached to the gill filaments, and *Parabomolochus bellones* moving about under the opercles and in the mouth, especially under the oral valves. No hosts had both *L. belones* and *L. tylosuri*, which occupy the same niche, although some host species may have both species of *Lernanthropus* on different individuals (see Host Specificity). The habitat of *P. bellones* includes the oral valves to which *Caligodes* is restricted. We found 12 *P. bellones-Caligodes* combinations on four species of needlefishes, mostly on *Ablennes* (8 records). Four of these *Ablennes* were large Gulf of Guinea specimens (418–530 mm. BL) with four or five species of copepods.

The absence or rarity of some copepod combinations is due partly to the influence of host specificity (or host ecology). Thus, there are no *Caligodes laciniatus-Lernanthropus belones* combinations because *Caligodes* is restricted to *Ablennes*, *Tylosurus*, and a few species of *Strongylura*, whereas *L. belones* is found primarily on a different group of *Strongylura*.

The absence of some other combinations is purely geographic: the eastern Pacific *Parabomolochus constrictus* and *P. ensiculus* cannot be

TABLE 8.—*Infestation of needlefishes by more than one species of marine copepod. Upper right half of table gives total number of individual needlefishes with a particular combination of copepods. Lower left half of table gives number of species of needlefish with the particular combination of copepods*

Species	*Parabomolochus*				*Nothobomolochus*		*Caligodes laciniatus*	*Lernanthropus*		*Colobomatus goodingi*	*Caligus* spp.
	belones	*sinensis*	*constrictus*	*ensiculus*	*gibber*	*digitatus*		*tylosuri*	*belones*		
	Number										
Parabomolochus bellones							12	26	65	37	6
P. sinensis						1		1			
P. constrictus			3				6	6	2	5	1
P. ensiculus			1						6		
Nothobomolochus gibber								1		4	1
N. digitatus	1	1					1	4	2		1
Caligodes laciniatus	4		3			1		36		22	6
Lernanthropus tylosuri	4	1	3		1	3	4			25	9
L. belones	3		1	2		1				13	
Colobomatus goodingi	5		3		2		3	3	2		6
Caligus spp.	3		1		1	1	2	4		3	
Total number of species of copepods found with each species.	6	2	6	2	3	5	6	8	5	7	7

373-320 O—70——11

found with *P. bellones*, *P. sinensis*, *Nothobomolochus gibber*, or *N. digitatus*, which are found only outside the eastern Pacific.

The rarity of some combinations may be related to competition between species of copepods. For example, we found no records of *Parabomolochus bellones* with *Nothobomolochus gibber*, only one record of *P. bellones* with *N. digitatus*, and none of *N. gibber* with *N. digitatus*. The geographical distributions of these three species overlap broadly, and they live in similar ecological niches on needlefish. On the basis of this lack of co-occurrence and on the greater abundance of *Nothobomolochus* from the eastern Indian Ocean to the central Pacific, we believe *Nothobomolochus* (and *P. sinensis*) may have evolved more recently and may be in the process of replacing *P. bellones* in the above areas.

Evidence also exists of competition between the two eastern Pacific species of *Parabomolochus*. *P. ensiculus* is usually found in the mouth, under the oral valves; *P. constrictus* is usually found under the opercles. There are only three records of co-occurrence on a specimen of needlefish. In at least one of these, two *P. constrictus* were under the opercles and one *P. ensiculus* was under the oral valves.

In this study, no two species of ergasilid copepods were taken from the same host individual although two ergasilids, *Ergasilus spatulus* and *Acusicola tenax*, were taken from what is now considered one species of needlefish, *Strongylura marina*, at different localities. Ergasilids are generally fresh-water copepods and other needlefish copepods are marine; it would be surprising, then, to find an ergasilid on the same host individual with a marine copepod. We found two such records, however, *E. inflatipes* and *Parabomolochus bellones* on a specimen of *S. senegalensis* from Ebzie Lagoon, Ivory Coast, and *E. coleus* and *Nothobomolochus digitatus* from *S. strongylura* from Sandakan Bay, Borneo.

We have shown that larger needlefishes are more likely to have specialized copepods than smaller needlefishes. Do they also have more species of copepods? Seven species of needlefishes had more than two species of copepods on the same individual host (table 7). A total of only nine specimens represented the four species of *Strongylura* with individuals having more than two species of copepods (three each): one *S. leiura* with *Caligodes*, *L. tylosuri*, and *N. digitatus;* three *S. notata* and four *S. timucu* with *Colobomatus*, *L. belones*, and *P. bellones;* and one *S. strongylura* with *P. sinensis*, *N. digitatus*, and *L. tylosuri*. The other cases of more than two species of copepod on the same host individual are indeed in the three large worldwide species: *Ablennes hians*, *Tylosurus acus*, and *T. crocodilus*. One specimen of *T. acus* had three species of copepods, two specimens had four; eight specimens of *T. crocodilus* had three species; three specimens of *Ablennes* had three species, three had four species, and two specimens had five. Seven species of copepods were involved in the 19 multiple combinations: *L. tylosuri* (17); *Colobomatus* (15); *Caligodes* (13); *Caligus* spp. (8); *P. bellones* (6); *P. constrictus* (4); and *N. digitatus* (1).

The two specimens of *Ablennes* with five species of copepods were both from the Gulf of Guinea: a 418-mm. BL specimen with 2 female *Caligodes*, 2 female *L. tylosuri*, 6 female *P. bellones*, 3 female *Caligus* sp. A, and 1 female *Colobomatus;* and a 530-mm. BL specimen with 25 female *Caligodes*, 1 male *L. tylosuri*, 3 female *P. bellones*, 1 male and 1 female *Caligus* sp. A, and 3 female *Colobomatus*.

The three *T. acus* specimens were 316, 374, and 535 mm. BL; the eight *T. crocodilus* 203, 227, 236, 261, 268, 300, 320, and 388 mm. BL; and the eight *Ablennes* 418, 455, 462, 483, 490, 508, 530, and 540 mm. BL. The species means (408, 275, 486) are greater than the mean body lengths of uninfested specimens, of all specimens examined (347, 250, 306), and of specimens infested by any particular species of copepod except the mean body length of *T. crocodilus* infested with *Caligodes*—303 mm. Thus, although the multiple-infested needlefishes are not the largest specimens of their species, they are larger than other groupings of their species.

Variation in Infestation With Time and Space

We have relatively few data on changes with time in infestation in a given population of needlefish. The best data come from the infestation by *Colobomatus goodingi* of three Bahamian samples of *Strongylura notata* taken in 1927, 1935, and 1963 (table 9). Four of six specimens from Crooked Island taken in 1927 were infested. Ten of 12 specimens collected at Bimini in 1935 were

TABLE 9.—*Sites of occurrence of* Colobomatus goodingi *in the cephalic lateral line canals of* Strongylura notata *from the Bahama Islands*

Locality and date	Specimens	Length range (BL)	Lower jaw		Interorbital		Upper jaw		Preorbital		Total
			R	L	R	L	R	L	R	L	
	Number	*Mm.*	*Number of specimens*								
Crooked Island:											
March 26, 1927	6	87–123	2	4	0	0	0	0	0	0	6
Bimini:											
Sept. 18–25, 1935	12	127–173	8	6	2	1	1	0	0	0	18
August 26, 1963	14	108–137	10	13	3	3	0	2	1	0	32
Total			20	23	5	4	1	2	1	0	56

infested, and all 14 specimens over 108 mm. BL were infested in 1963. Two specimens (76–80 mm. BL) from Crooked Island and five (58–65 mm. BL) from Bimini were uninfested in the 1963 collection. The average number of *Colobomatus* sites per fish (over 80 mm. BL) was 1.0 in 1927, 1.5 in 1935, and 2.6 in 1963. Thus, in this small sample, relative infestation seemed to be increasing over this time span.

Information is more plentiful on geographic variation in infestation. For example, the incidence of infestation by *Parabomolochus bellones* generally decreases from the Atlantic to the western Pacific (tables 4 and 5), probably because of competition with *P. sinensis* and the two species of *Nothobomolochus*.

The infestation of *Platybelone argalus* with juvenile stages of *Caligus* sp. varies widely from area to area. In the eastern Atlantic 42 percent of the *P. argalus* were so infested (table 4); this figure reaches nearly 100 percent if the uninfested populations at some island groups (Azores, Cape Verdes, Ascension, and St. Helena) are eliminated. Of 46 *P. a. annobonensis* taken at Annobon Island in 1964 and 1965, all but 3 had juvenile *Caligus* attached to the fins, and as many as 13 copepods were picked off a single needlefish. However, none of 11 *P. a. annobonensis* taken at the nearby island of Fernando Poó had any copepods.

Another clear example of geographic differences in infestation was found in *Tylosurus acus*. All populations were infested with *Caligodes*, *L. tylosuri*, and *Colobomatus* except for the Mediterranean *T. acus imperialis*, on which no copepods were found. This gross difference in infestation of the Mediterranean population of *T. acus* from the western Atlantic *T. a. acus* and the Gulf of Guinea *T. a. rafale* lends support to the taxonomic distinctness of the Mediterranean population.

Rather large amounts of interarea variation appear in the infestation of *Ablennes hians*, *Tylosurus acus*, and *T. crocodilus* by *Caligodes laciniatus*, *Lernanthropus tylosuri*, and *Colobomatus goodingi*. Some of this variation is no doubt due to differences in sizes of the hosts, larger hosts being more likely to be infested; some is definitely correlated with geography. For example, *Colobomatus* was found on only two large western Atlantic *Ablennes* and on no Indian Ocean specimens, yet it was very common in the Gulf of Guinea (41 percent). Interestingly, a similarly low rate of infestation by *Lernanthropus tylosuri* was found in the western Atlantic and the Indian Oceans.

At present, we can offer no explanation for these differences in infestation. The geographic differences are important in indicating restricted amount of interchange between populations of needlefishes and so serve to point out those populations that may be taxonomically distinct.

Nature of the Symbiotic Relationship

It is difficult to assess accurately the true nature of the relationship that exists between most species of "parasitic" copepods and their hosts. In the absence of measurable or observable damage to host tissue, it is open to question whether or not an organism is parasitic in the strict sense or if the relationship is commensalistic or mutualistic. For purposes of this discussion parasitism is defined as a relationship in which the host suffers tissue damage or is impeded in efficiency because of the presence of "parasites." Commensalism is that relationship whereby the host provides shelter (protection) or food to the "commensal" and neither suffers hardship nor benefits. Mutualism is defined as that relationship whereby both organisms benefit. Unless exhaustive life history observations are made,

all of these situations are difficult to assess except where damage or reduced efficiency to the host can be demonstrated.

Colobomatus goodingi is clearly parasitic. The host reaction is evidence that this copepod is causing some damage to the needlefish. The capsules formed on the jaw of the host must cause hydrodynamic interference with swimming and hence with the food-getting process.

Caligodes laciniatus must reduce the efficiency of the oral valves. We have examined specimens in which the oral valves were literally bulging with this parasite. As in all other caligid copepods, its mandibles are adapted for cutting and rasping and it undoubtedly feeds on the hosts' tissues. Usually tissue damage was not observed, and it is probable that caligid copepods inflict serious physical damage to their hosts only when present in great numbers.

No damage to the host tissue was apparent from adult *Caligus*, but they have to be considered parasitic because their mouth parts are adapted to feed on tissue. The fins of *Platybelone argalus* from Annobon Island that were infested with chalimus stages of this genus were deformed (Collette and Parin, 1970). The damage probably would reduce the efficiency of the fins.

No observable injury was caused by the presence of *Lernanthropus* on the gill filaments. Because the mouth parts are adapted for cutting and rasping, however, they must inflict some tissue damage. As with many other species of parasitic copepods, small numbers of these may be tolerated by the hosts with little damage or discomfort.

We cannot demonstrate that ergasilids were causing injury to the gill filaments to which they were attached but reports (Dogiel, Petrushevski, and Polyanski, 1961, p. 315; Rogers, 1969, p. 445), cite severe damage to host tissue when the parasites are present in large numbers. Because of this capability they must be considered parasitic.

The only group of needlefish copepods which we do not consider parasitic are the bomolochids. It seems likely to us that this relationship is commensal or even mutualistic. Bomolochid copepods are not highly modified in comparison with the other copepods considered here. They are able to move about freely within their preferred habitats (oral or gill chamber) and may actually clean these areas of detritus, accumulated mucus, or other undesirable matter. Because they do not attach to the host securely (unlike most of the other species considered here) they probably do not feed on host tissue. To do so would require the ability to maintain one position for a long period of time, and, in view of their weakly developed mouth parts, they are probably not able to do this.

Until we know more of the feeding and interference effects of copepods found on fishes the question of relationship to the host of most of them cannot be answered definitively.

ADDENDUM

Subsequent to the completion and submission of this manuscript the junior author examined additional material in several Australian museums. The additional new records are as follows (none of these are included in the maps, tables, or any portion of the main body of this paper):

Neoergasilus sp. (probably new) from *X. cancila*, Madras, India.

Ergasilus coleus from *S. strongylura*, Arnhem Land, Australia.

Ergasilus semicoleus from *S. krefftii* from Flinders River, Queensland, Australia.

Parabomolochus bellones from *Lhotskia gavialoides* (2 collections), New South Wales: *S. strongylura*, Gulf of Carpentaria and Onslow, Australia: *S. leiura*, Gulf of Carpentaria: *A. hians*, Port Stevens, New South Wales, Australia.

Nothobomolochus digitatus from *S. strongylura*, Onslow, Gulf of Carpentaria, Northern Territory (all Australia); Bombay, India.

Caligodes laciniatus from *L. gavialoides* (2 collections), New South Wales: *S. leiura*, Gulf of Carpentaria: *T. crocodilus* (5 collections), Percy Is. and Hayman Is., Queensland; Murray Is., Torres Strait; Gulf of Carpentaria; Tonga Is.

Lernanthropus tylosuri from *S. leiura*, Gulf of Carpentaria (2 collections) and Queensland; *S. strongylura*, Bombay, India; *T. crocodilus*, Tonga Is.

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SOME CHEMICAL AND PHYSICAL PROPERTIES OF TWO TOXINS FROM THE RED-TIDE ORGANISM, *GYMNODINIUM BREVE* [1, 2]

BY DEAN F. MARTIN [3] AND ASHIM B. CHATTERJEE [4]

ABSTRACT

A procedure is given for isolating and purifying two toxins (substance I and II) from cultures or blooms of *Gymnodinium breve*. In vitro studies of acetylcholinesterase activity show that the major toxin is not a cholinesterase inhibitor. On the basis of the infrared data the properties of toxin samples isolated from blooms of *G. breve* appear to be identical to those from axenic cultures.

Substance II is a light yellow, low-melting solid. Carbon, hydrogen, and phosphorus are present; sulfur, chlorine, bromine, and nitrogen are absent. The percentage composition is given for carbon, hydrogen, oxygen, and phosphorus; an empirical formula of $C_{50}H_{102}O_{17}P$ is indicated by the analytical data. A molecular weight of 650 was obtained from a sample of substance II.

Substance II was characterized by the absorption spectra (ultraviolet, infrared), by the nuclear magnetic resonance spectrum, and by the specific optical activity. These observations and the mass spectrogram provide useful structural information.

Substance I was characterized by the infrared spectrum which indicated the presence of a carbonyl group. Not enough of substance I was isolated for an elemental analysis.

Evidence for a causal relation between blooms of the Florida red-tide organism, *Gymnodinium breve*, and animal intoxication once rested on seasonal and geographic correlations of these events. The value of the correlation was limited because of the presence of accompanying bacterial species with ichthyotoxic properties (Bein, 1954). The relation was established by Ray and Wilson (1957), who showed that cultures of *G. breve* killed fish, and by McFarren, Tanabe, Silva, Wilson, Campbell, and Lewis (1965), who isolated a ciguateralike poison from oysters and clams (taken from the area in which a bloom occurred), from a bloom of *G. breve*, and from laboratory cultures of *G. breve*.

Before the present study, comparatively little was known about the chemical and biochemical properties of the toxin of *G. breve*. Starr (1958) described attempts to characterize the toxin through bioassays in which mullet and guppies were used to compare the potency of different toxic preparations.

Sasner (1965) reported that the toxin was an endotoxic substance which was soluble in water and ethyl alcohol, insoluble in chloroform, heat labile, acid stable, and slowly dialyzable. The toxic materials in his extracts affected all excitable membranes studied: sciatic nerve, sartorius nerve-muscle preparations, and skin from the leopard frog, *Rana pipiens;* the anterior byssus retractor muscle of Californian mussel, *Mytilus californianus;* and the leg nerves of the spider crab, *Loxyrhynchus* sp. In all cases, the membranes had been rendered unexcitable to electrical stimulation. The toxin caused depolarization and complete loss of the resting potential. According to Sasner (1965), the physiological effects of *G. breve* toxin closely paralleled those of a British gymnodinoid, *Gymnodinium veneficum* (Abbott and Ballantine, 1957). The toxin produced paralysis but was different from a curare-type (synaptic blocking agent) toxin, which is characteristic of *Gonyaulax catenella* (Schantz, Lynch, Vayvada, Matsumoto, and Rapoport, 1966).

A number of toxigenic algae are known; Shilo (1967) included species of dinoflagellates, certain blue-green algae (e.g., *Microcystis aeruginosa*) and several species of Chrysophyta (e.g., *Prymnesium parvum*). Before the present study, however, few of the algal toxins seem to

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have been chemically characterized. Saxitoxin (the toxin of *G. catenella*) has a molecular weight of about 370 and a purine (nitrogenous) base (Schuett and Rapoport, 1962; Schantz et al., 1966). The toxin obtained from *M. aeruginosa* is a cyclic polypeptide composed of 10 amino acid moieties, including D-serine (Bishop, Anet, and Gorham, 1959; Gorham, 1960). Prymnesin, an endotoxin from *P. parvum*, is a glycolipid with a molecular weight of about 23,000 (Paster, 1968). The lipid portion is composed of four long chain acids (myristic, stearic, palmitic, and oleic) and the polysaccharide portion of glucose, mannose, and galactose. The toxin (s) isolated from *G. breve* is thus one of the few algal toxins to be chemically characterized.

MATERIALS AND METHODS

REAGENTS

Most reagents used in this study were analytical grade, and all solvents were Baker [5] analyzed reagents with the following exceptions: Silica gel (grade 62, mesh 60–200) used for chromatography was obtained from Grace Davison Chemical, Baltimore, Md.; bone charcoal was B & A reagent grade; carbon tetrachloride used for spectra was GC-spectrophotometric reagent grade.

SOURCE OF *GYMNODINIUM BREVE*

Organisms were obtained in two ways. Axenic cultures of *G. breve* were obtained from W. B. Wilson (Wilson, 1965) and were subcultured in B-5 medium (Wilson, 1966). Water samples were collected during an outbreak of *G. breve* in the fall of 1967 near Big Pass, off Sarasota, Fla.

PROCEDURE FOR ISOLATION OF TOXINS

We isolated two substances by using the following procedure. Water from the bloom of *Gymnodinium breve* or from laboratory culture media (1×10^6 cells/liter) was adjusted to pH 4.0 by addition of a small quantity of concentrated (12 *M*) hydrochloric acid. Two-liter portions of the solution were then extracted in Fernbach flasks with 30 ml. of chloroform. The mixture was agitated with a mechanical stirrer; the top of the flask was covered with a slotted cardboard to avoid splashing. Each batch was stirred vigorously for 15 minutes and allowed to settle in a modified separatory funnel for 20 minutes. Water from the top layer was discarded by a side tap, and the chloroform extract (substance II) was taken out from the bottom and stored. The combined chloroform extracts were associated with an upper thick interfacial layer consisting of very small bubbles and containing substance I. This layer containing the bubbles was highly toxic to fish. Extracts from a particular batch of water were always kept in separate containers, stored in a refrigerator.

PURIFICATION

The two layers, i.e., the chloroform extract and the interfacial layer, were treated separately.

The clear chloroform layer (substance II) was separated, concentrated, and then purified by column chromatography. We used a separatory funnel to separate the chloroform from the interfacial layer. Generally, an extract containing an appreciable amount of toxin was intensely yellow. The chloroform layer (30 to 40 ml.) was concentrated in a rotary evaporator to one-tenth of its volume, and then passed through a silica-gel column (4 cm. long, 1 cm. diameter) at a rate of 18 to 20 drops per minute. Yellow material, with a greenish-yellow band above it, was adsorbed on top of the column. The colorless chloroform effluent was evaporated (rotary evaporator), and the yellow oily residue was nontoxic to fish. The column was next treated with methylene chloride (four 10-ml. portions), and the yellowish-green band was eluted, leaving the deep brown band on the silica gel. The effluent was evaporated in cold, and the greenish residue obtained was nontoxic to fish. Finally, the brown band was eluted with two 2- to 3-ml. portions of absolute ethanol. The deep yellow effluent was evaporated slowly in a vacuum desiccator. The residue was toxic.

The thick yellow residue (substance II) was dissolved in carbon tetrachloride and purified further. The solution was stirred with bone charcoal and filtered. The colorless carbon tetra-

[5] References to trade names or suppliers in this publication do not imply endorsement of commercial products.

chloride filtrate was evaporated slowly in a desiccator and yielded a light yellow viscous semisolid that was highly toxic.

The interfacial layer (substance I) was separated and the toxin was isolated by removal of solvent. The layer was composed of bubbles trapped in chloroform; normally, a large amount of salt water was associated with it. We washed this layer twice with 250-ml. portions of dilute hydrochloric acid solution (pH 3.5–4.0) in a separatory funnel. The organic layer was collected in long test tubes and allowed to stand over silica gel for drying. Thus purified, substance I was mostly free from sodium chloride. When the organic material was sufficiently dried, flaky dark-green suspended matter was found in the test tubes. Contents of the tubes were transferred to a flask, and the volume was increased 25 percent with absolute ethanol. The mixture was stirred 4 hours, cooled, and filtered. The residue was not toxic. The filtrate was cooled in an ice-water bath and evaporated under reduced pressure.

The residue (substance I) was dissolved in ethanol and purified further. The ethanol solution was cooled in a Dry-Ice bath, stirred with bone charcoal, and filtered. When the filtrate was evaporated, the residue was a toxic, yellowish, oily solid.

THE TOXIN UNIT

One *Gymnodinium breve* fish-kill unit was defined arbitrarily as the amount of toxin per 50 ml. of sea water which under standard conditions killed a 3.0- to 3.5-g. (6- to 7.5-cm.) longnose killifish, *Fundulus similis*, in 7 to 8 minutes. The standard conditions included 50 ml. of test solution in a 400-ml. beaker, controlled temperature (23°±2° C.), and appropriate salinity (32–33 p.p.t.) and pH (8.0–8.2).

EFFECT OF TEMPERATURE

The toxin (substance I in interfacial layer) was maintained at room temperature, 23°±2° C., and periodically tested for potency. The results, summarized in table 1, indicate that a solution of the toxin is stable at room temperature for at least 96 hours.

All toxicity was lost when the sample in chloroform-water solution was heated to 110° C.

TABLE 1.—*Temporal stability of crude toxin (substance I) from* G. breve *at room temperature*

Time	Volume of toxin [1]	Amount of water taken	Length of fish [2]	Approximate weight of fish	Death time	Fish-kill unit
Hours	*Drops*	*Ml.*	*Cm.*	*G.*	*Minutes*	
0	2	50	3.8	1.1	5	1
1	2	50	3.8	1.2	5–6	1
4	2	60	3.8	1.5	5–6	1
8	2	75	3.8	2.0	5–6	1
24	2	75	3.8	2.0	6–7	1
30	2	100	6.4	3.0	6	1
96	2	50	3.5	1.1	6–7	1

[1] Control: two drops of chloroform in same volume of sea water. No effect on fish within 120 minutes.
[2] *Fundulus similis.*

for 5 minutes, and the loss in weight of the sample was 0.3887 g. or 97.5 percent. At this temperature, volatilization of chloroform and water would be expected.

In addition, presumably these data indicate either the volatility or the ease of decomposition of the toxin. Attempts to detect decomposition products with gas chromatography were unsuccessful. An Aerograph vapor phase chromatography unit, equipped with Carbowax 400 column and a thermal detector, was used. Column temperature was maintained at 55° C. The amount of toxin (substance I in ether) may have been insufficient to detect.

Attempts were made to measure the volatility of the sample as follows: One fish was placed in each of two beakers (under the conditions previously defined for the toxin unit). The two beakers were placed in a closed system, and the first beaker was treated with 1 fish kill unit of toxin (substance I). Four minutes later a stream of nitrogen was passed through solution in the first beaker, forcing any evolved gases to pass through the second beaker. The fish in the first beaker died after 6 minutes; the one in the second beaker was unaffected for 12 minutes, after which time the experiment was discontinued. We concluded that the toxin was not volatile at atmospheric pressure at room temperature. However, a loss of toxicity under reduced pressure (when a rotary evaporator is used) was amply indicated.

ELEMENTAL QUALITATIVE ANALYSIS

Purified samples of toxin (substance I and substance II) were fused with sodium and decomposed with water, and the solution was analyzed for nitrogen, sulfur, halogen (chlorine,

bromine, or iodine), and phosphorus by the procedures of Vogel (1956). Positive tests were obtained only for phosphorus. In all cases, the results were compared with known compounds to verify the test.

ELEMENTAL QUANTITATIVE ANALYSIS

Semimicro quantitative analyses for carbon, hydrogen, and nitrogen were performed by Peninsular Chem Research, Inc., Gainesville, Fla. (table 2).

Organic phosphorus was determined by a conventional method (Martin, 1968). The calibration curve (fig. 1) was prepared with a phosphorus standard (disodium *p*-nitrophenylphosphate). Exactly 0.89 mg. of substance II was decomposed and diluted to 50 ml.; two 25-ml. portions had absorbances of 0.058 and 0.055, which corresponded to 1.41 percent P. A second analysis was performed similarly with 0.99 mg. of substance II, except that 6.968 μg. of phosphorus (as phosphorus standard) was added; total absorbances of 0.115 and 0.118 were obtained, which gave a corrected value of 1.35 percent P.

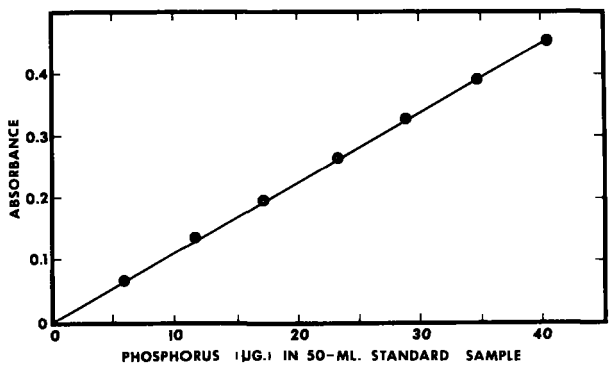

FIGURE 1.—Calibration plot for organic phosphorus determination. Standard sample prepared by decomposition of 9.8 mg. of disodium *p*-nitrophenylphosphate, followed by dilution to 50 ml. with triple-distilled water at 705 mμ.

TABLE 2.—*Elemental quantitative analysis of substance II (bloom sample)*

Sample	Carbon	Hydrogen	Nitrogen	Phosphorus	Oxygen
			Percent		
1.....	47.05	6.94	0.00	0.00	0.00
2.....	49.60	7.60	[1](0.6)	1.41	[2] 41.4
3.....	0.00	0.00	0.00	0.00	41.8

[1] Not analytically significant.
[2] Calculated by difference from 100 percent total.

Total oxygen was determined by Schwarzkopf Microanalytical Laboratory, Woodside, N.Y. Exactly 0.200 mg. of toxin sample produced 0.115 mg. of carbon dioxide.

MOLECULAR WEIGHT

The molecular weight of substance II (bloom sample), determined by Galbraith Laboratories, Inc., Knoxville, Tenn., by vapor-pressure osmometry, was 650 (chloroform solvent, 0.03 *M*).

ABSORPTION SPECTRA

The carbon tetrachloride solution of substance II from the bloom sample had no absorption in the visible region of the spectrum; its absorption maximum was at 269.5 to 270 mμ (2.5 mg./3 ml. in CCl_4) in the ultraviolet region. When the solution was diluted, the absorption maximum broadened and was 265 to 270 mμ for the most dilute solution (table 3).

The prominent absorption bands of the infrared absorption spectra of various toxin fractions (as carbon tetrachloride solutions) were determined (table 4). Tentative assignments are also indicated and are compared with standard values given by Bellamy (1958).

TABLE 3.—*Ultraviolet absorption of carbon tetrachloride solutions of substance II at 269 mμ*

Concentration	Maximum absorbance
(Mg./1 ml. CCl_4)	
0.833	1.020
.556	0.730
.371	0.490
.247	0.340

The similarity of substance II samples isolated from bloom water and from culture medium is indicated by the infrared data obtained with a Perkin-Elmer 337 infracord. Substance I could not be isolated in sufficient quantity from culture medium for analysis. The bloom sample of substance I seems to be different from the bloom sample of substance II; the infrared spectrum of the former indicates the presence of a carbonyl group, whereas the spectrum of the latter does not.

TABLE 4.—*Characteristic infrared absorption frequencies of three toxin samples dissolved in CCl_4*

Frequency [1]	Possible assignment	Literature value [1]
	Substance II (bloom sample)	
3,000 (vs)	C-H (paraffinic) (unsaturated)	3,000 (s)
2,400 (s)	P-H	PH_3, 2,327–2,421
1,422 (br,s)	PC_6H_5	1,450 (s), 1,000 (m)
	−O	
1,266 (s)	+P (OR)$_2$	1,265 (s)
1,217 (vs)	P-OC_6H_5	1,218 (P-O-aromatic) (s)
920 (m)	P-O-P	970–940 (m)
667 (vs)	P-C (aliphatic)	750–650 (s)
	Substance I (bloom sample)	
2,940 (s), 2,865 (s)	−CH_3	2,962, 2,872 ± 10 (s)
2,905 (s)	−CH_2-	2,926, 2,553 ± 10 (s)
1,730 (m)	−CO-	1,700–1,750 (s)
1,460 (m)	−C-CH_3	1,450 ± 20 (m)
	−O	
1,265 (s), 1,010 (s)	+P (OR)$_2$	1,265 (s), 1,050–1,000 (s)
1,210 (s)	$(CH_3)_2$-C-R	1,250–1,200 (s)
1,080 (s)	−CH_2-O-CH_2	1,150–1,160 (vs)
1,010 (s)	cyclopropyl	1,020–1,000 (m)
	Substance II (culture medium sample)	
2,950 (s)	−CH_3	2,962, 2,872 ± 10 (s)
2,900 (s)	−CH_2-	2,926, 2,553 ± 10 (s)
	−O	
1,263 (s)	+P (OR)$_2$	1,265
1,215 (vs)	POC_6H_5	1,218 (P-O-aromatic) (s)
667 (vs)	P-C (aliphatic)	750–650 (s)

[1] Intensity abbreviations: (vs) very strong; (s) strong; (m) medium; (br) broad.

NUCLEAR MAGNETIC RESONANCE SPECTRA

The background of nuclear magnetic resonance spectroscopy was given by Pople, Schneider, and Bernstein (1959). The spectrum was obtained for a 5-percent (w/v) solution of purified substance II (bloom sample) in $CDCl_3$. The spectrum had two signals: one at 6.31τ and the other at 9.38τ. Tetramethylsilane (TMS) was used as an external, not an internal, standard to avoid contaminating the sample.

A spectrum was also obtained of a 1-percent (w/v) carbon tetrachloride solution (2.5 mg. of substance II in 0.3 ml. of solvent). Again, an external standard TMS was used. Signals were obtained at 6.4 (singlet) and 9.45τ (singlet, triplet).

A signal at 6.3τ may be ascribed to a methylene group attached to an electronegative atom or moiety, e.g., oxygen. The signal at 9.38τ represents an unusually high tau value. One possibility is contamination from silicone grease, though this seems unlikely in view of the precautions taken. The signal intensity suggests a second possibility—that the signal can be ascribed to a methylene in a strained ring. For example, cyclopropane $(CH_2)_3$ has a signal at 9.778τ. The presence of a cyclopropyl moiety seems unlikely because of the absence of prominent absorption peaks in the 1,000 to 1,200 cm.$^{-1}$ region of the infrared region (Yukawa, 1965). For comparison, a methylene group in an aliphatic hydrocarbon would produce a signal at 8.75τ.

OPTICAL ACTIVITY

A Bendix Corporation NPL automatic polarimeter, Type 143A, fitted with a mercury-green lamp (546.1 mμ), was used for all optical activity measurements. The precision of this instrument is ±0.0002°.

The instrument was calibrated with sucrose solution (table 5), by the following technique. Exactly 100 divisions (1 complete rotation) on the fine adjustment zero-control knob corresponds to 10 m.° (=0.01 degree) of rotation of the plane of plane-polarized light. The reading for pure solvent (for a given measurement) was adjusted to zero by using the fine adjustment knob, and the reading on the knob was recorded. Next, the test solution was placed in the cell and the galvanometer pointer was returned to zero. The reading on the knob was recorded. The difference between the two readings (for the solvent and that for the test solution) was converted to millidegrees of observed rotation, α (100 divisions=10 m.°).

For all test solutions, the specific rotation $[\alpha]^{25°}_{546m\mu}$ was calculated from the usual relationship (Vogel, 1956): $[\alpha] = 100\,M/(\ell pd)$, where α is the observed rotation, ℓ is the length of the light path, (0.1 dm), p is the concentration

TABLE 5.—*Specific optical activity of toxin samples at 25° C. and 546 mμ*

Sample	Sign of rotation	Observed rotation	Specific activity
		α, m.°	$[\alpha]^{25°}_{546m\mu}$
1. Sucrose solution, (3.062%)	+	241.0	78.38
2. Substance II in absolute ethanol			
a. After column chromatography	+	2.25	68.2
b. After charcoal treatment	+	3.5	47.0
3. Sample 2b (above) after evaporation of solvent in vacuum desiccator and resolution in absolute ethanol	−	0.3	4.0

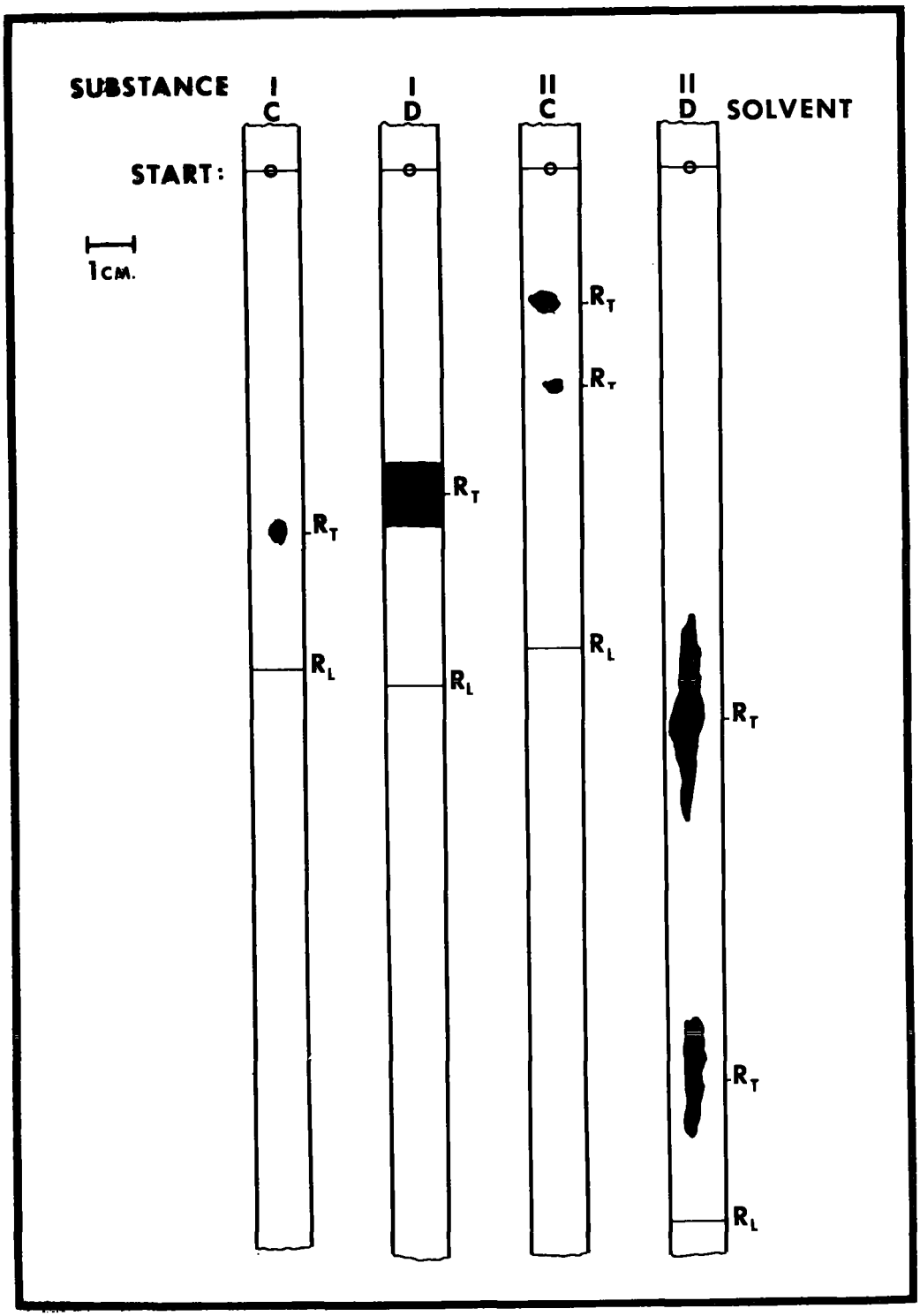

FIGURE 2.—Descending paper chromatograms of toxins (see table 6).

(g. solute/100 g. solution), and d is the density (g./ml.) of the solution (table 5).

The optical activity measurements have several points of interest. First, the sample of substance II is optically active and is dextrorotatory. Some loss of optical activity seemed to occur during the purification scheme (sample 2a versus 2b, table 5). This loss may be due to the removal of a volatile component, as indicated by the further loss of optical activity accompanying evaporation (sample 2b versus 3). It appeared, qualitatively, that there was no loss of toxicity associated with the loss of optical activity.

CHROMATOGRAPHY

TLC (thin-layer chromatography) and paper chromatography (Heftmann, 1967) were used to characterize the toxin and to determine if the purified toxin contained one component or two, as suggested by molecular weight versus weight data from the empirical formula.

When an Eastman chromatogram (for TLC) with silica-gel absorbent was used, only one spot was located (with ultraviolet light) with two different solvent mixtures. The R_f values [6] indicate that the effect of change of solvent polarity was small. The behavior of the toxin with TLC (silica gel) was consistent with column chromatography, i.e., only one fraction was obtained.

TABLE 6.—*R_f values for toxin chromatograms* [1]

Chromatogram	Toxin sample	Solvent mixture	Rf [2]
TLC (silica gel) ...	Substance II (bloom)	A	0.89
Do	do	B	.90
Paper	Substance I (bloom)	C	.72
Do	do	D	.63
Do	Substance II (bloom)	C	.83, .38
Do	do	D	.85, .52

[1] Solvent mixture A, 10 percent (v/v) chloroform-absolute ethanol; solvent mixture B, 10 percent (v/v) chloroform-isoamyl alcohol; C, absolute ethanol; D, isoamyl alcohol.

[2] The Rf value is defined as the ratio of the distance traveled by a substance (RT) to the distance traveled by the solvent (RL).

Another system, paper chromatography, was selected to see if more than one component was present in the fraction. Descending paper chromatography was effected with different solvents (table 6). The chromatograms were run for 5 hours, after which the paper strips were dried, developed with a mixture of minhydrinphenol methyl cellosolve mixture, and washed with dilute sodium hydroxide solutions. Two components were indicated (fig. 2, table 6). R_f values for one component seemed independent of solvent polarity; the R_f values for a second were affected by change in solvent polarity.

[6] The Rf value is defined as the ratio of the distance traveled by a substance (RT) to the distance traveled by the solvent (RL).

ACETYLCHOLINESTERASE ACTIVITY

A potentiometric determination (Jensen-Holm, Lausen, Milthers, and Moller, 1959) was used to measure enzyme activity. The brains of five sheepshead minnows, *Cyprinodon variegatus*, were placed in 12 ml. of distilled water, cooled in an ice-water bath, and homogenized for 40 seconds with an ultrasonic macerator operated at full power. The test solution was prepared by diluting 2.0 ml. of the homogenate to 4.5 ml. with distilled water. The pH was adjusted to 7.8 with 0.02 N sodium hydroxide solution, and 0.05 ml. of substrate (0.1 M acetylcholine iodide) was added. The cholinesterase activity was determined poten-

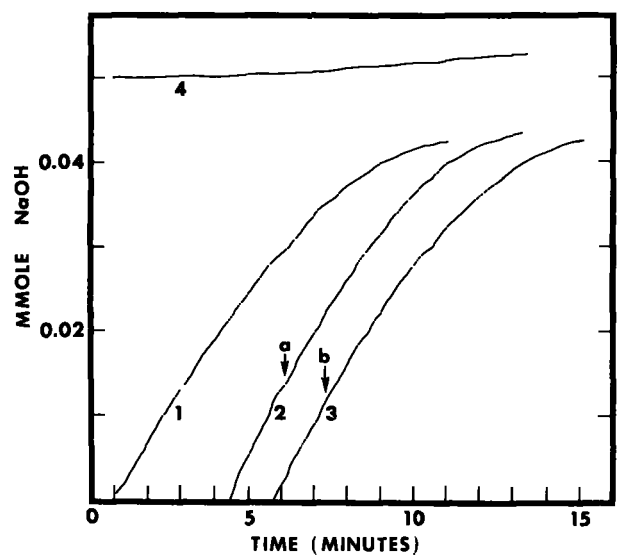

FIGURE 3.—Potentiometric determination of cholinesterase activity, micromoles of sodium hydroxide added as a function of time (minutes). Curve 1, standard run; curve 2, 0.02 ml. of toxin solution added at point a; curve 3, 0.4 ml. of toxin solution added at point b; curve 4, spontaneous acid liberation in absence of homogenate.

tiometrically at 38° C. with an automatic titrator operated as a pH-stat unit. Enzyme activity was expressed as micromoles of sodium hydroxide added per minute (fig. 3) to a pH 7.5 end-point.

The activity of the toxin was tested as follows. In a succeeding trial, the enzyme activity was measured again, and after 2 minutes an aqueous solution of the toxin (substance II dispersed in water by means of the ultrasonic macerator) was added. The determination curves (fig. 3) indicate the addition of 0.2 ml. or 0.4 ml. of toxin solution has no effect on homogenate activity. The activity of the toxin solution was verified: 0.2 ml. of solution (*ca.* 0.15 mg. substance II) added to 30 ml. of sea water caused death of sheepshead minnows (5.5 cm., 4.1 g.) within 3 minutes.

MASS SPECTRAL ANALYSIS

The mass spectrum of substance II (bloom sample) was obtained by using the following conditions: ionizing voltage 70 e.v. pressure 1.5 $\times 10^{-6}$ mm. Hg., and temperature 50° C. (table 7).

TABLE 7.—*Mass-charge ratios (m/e) and relative abundances from mass spectral analysis of substance II.*

m/e	Relative abundance	m/e	Relative abundance
27	11.0	151	37.0
31	30.9	153	13.5
42	54.1	155	13.5
45	80.0	157	13.5
57	62.7	160	30.8
59	77.5	240	14.9
63	19.6	258	8.6
67	22.1	266	6.3
69	54.0	290	9.0
72	60.6	301	6.3
83	60.1	309	5.0
86	56.5	310	5.0
100	45.5	311	5.0
102	24.7	319	5.0
107	16.1	320	5.0
121	17.2	321	5.0
124	18.1	333	4.8
128	24.8	334	4.8
131	15.4	335	4.8
138	15.1	348	4.8
141	15.1	349	4.8
143	15.1	[1] 350	4.8

[1] The amplified scale spectrum (100 times regular intensity) indicates stable species (with relative abundance of less than 1) at m/e of 375, 390, 450, 418, 440, 477, 508. Maximum relative abundance is 80.

SOME CHEMICAL CHARACTERISTICS AND STRUCTURAL FEATURES OF THE TOXIN

The purpose of the present study was to isolate the toxins of *Gymnodinium breve* blooms and cultures and to determine the chemical and physical properties of these toxins. During the course of the study, sufficient information was obtained from these properties to indicate some structural features of the toxins. The topics will be considered in order; a review of the chemical characteristics of the toxin is necessary to understand the structural characteristics. Unfortunately, not enough substance I was isolated to evaluate its chemical characteristics, and most of the discussion must be confined to substance II.

CHEMICAL CHARACTERISTICS

Several results of the present study are consistent with those of previous investigators.

First, several workers (McFarren et al., 1965; Sasner, 1965; Cummins, Stevens, Huntley, Hill, and Higgins, 1968) have also found two (or more) toxins which differ in solubility and other physical properties. In the present study, two toxins—substances I and II—were separated from *Gymnodinium breve* bloom water. Both have been separated from cultures of *G. breve,* although substance I was isolated only in trace quantities and could easily have been missed.

Secondly, the major toxin (substance II) is essentially an endotoxin. This determination was made in the present study by dividing a 1–1. sample of *G. breve* culture into two portions and extracting the medium before (portion A) and after (portion B) the cells had been removed by gravity filtration. Detectable amounts of toxin could be isolated from portion A but not from portion B. An alternative possibility, complete adsorption of the toxin in the filter paper, has not been observed.

Thirdly, the major toxin of *G. breve* may be a neurotoxin, but it evidently does not inhibit cholinesterase activity in vitro.

Fourthly, the toxins (substance I or II) seem to volatilize under reduced pressure, although the toxin is not readily volatilized from aqueous solution by a stream of nitrogen.

The study provided the following results that apparently have not been reported previously.

1. The major toxin (substance II) isolated from a bloom of *G. breve* appears to be similar to that isolated from cultures of *G. breve.* This

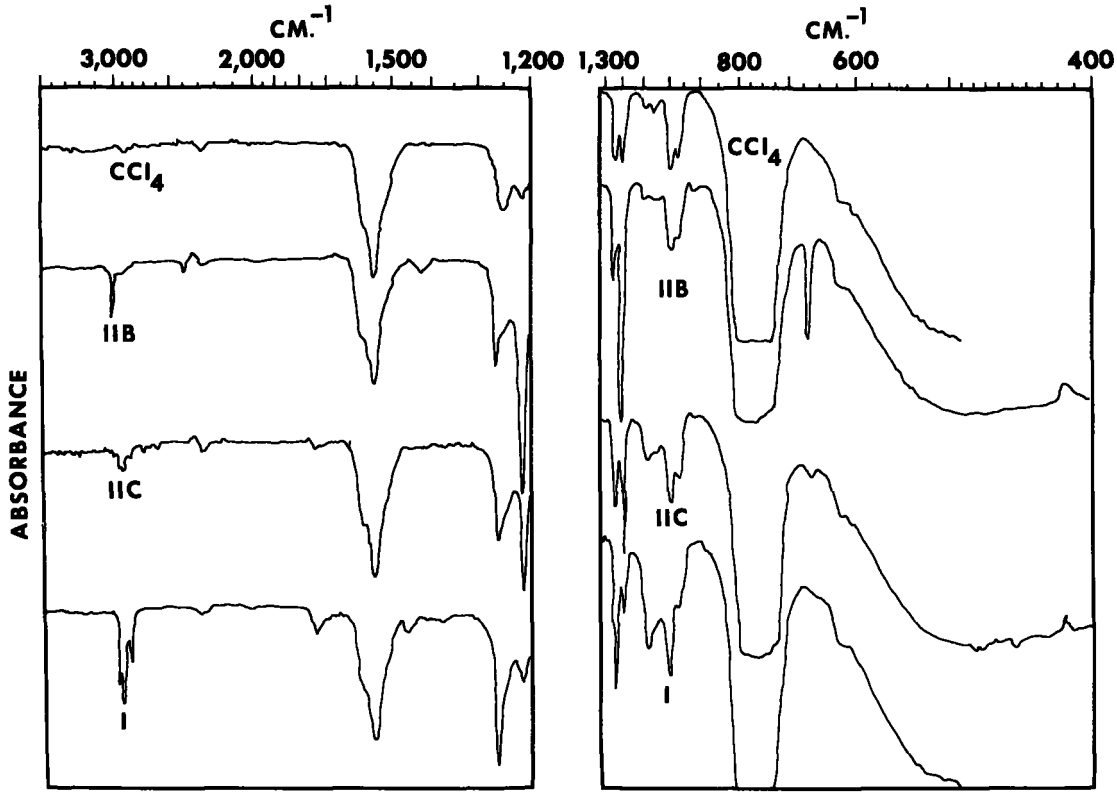

FIGURE 4.—Infrared absorption spectra of toxins in CCl_4. The instrument used provides spectra in two regions, low and high wavelength, as indicated. (Reference cell contained air.) Key to spectra; CCl_4, pure solvent; IIB, substance II (bloom sample); IIC, substance II (culture sample); I, substance I (bloom sample).

observation is based on a study of infrared spectral data (table 4). These data also indicate that substances I and II differ; notably a carbonyl group is indicated by the spectrum of substance I (fig. 4) but not by the spectrum of substance II.

2. The major toxin (substance II) does not contain nitrogen according to qualitative and quantitative analysis (table 2). This appears to be the first report of a phosphorus-containing toxin isolated from dinoflagellate blooms, a fact that is of considerable interest because organophosphorus compounds have been used as model compounds in the study of factors controlling nerve activity (Nachmansohn, 1961).

3. An empirical formula of $C_{90}H_{162}O_{17}P$ was calculated from the mean values of the quantitative elemental analytical data of substance II (table 2). Substance I could not be isolated in the quantity required for elemental analysis. As usual, the validity of the empirical formula is governed by the validity of the elemental analysis. In this instance, the reliability is indicated by replication of carbon and hydrogen analysis for different samples. The phosphorus analysis is the limiting factor in the accuracy of the formula. The results with a "spiked" sample suggest decomposition is complete; the values are within the experimental error.

4. A molecular weight of 650 was determined for substance II. This is about one-half the value of the empirical formula weight (1,545) and indicates each unit of substance II exists as two particles in chloroform (and presumably in other polar solvents). The observation gives no information about the relative sizes of the two particles. The two particles must be similar in properties because only one band is obtained with chromatography (thin-layer or column) using silica gel. Also, two bands indicative of two components were obtained when substance

II was subjected to descending paper chromatography (table 6).

5. Three methods have been devised for detecting the toxin. These are: a toxicity test under a standard set of conditions; a spectroscopic test using the absorbance of a CCl_4 solution at 270 mμ (ε obs.=790, ε calc.=1900)[7]; and the optical activity test that detects certain centers or units of asymmetry.

6. Substance II is optically active, which indicates a center or molecular unit of asymmetry (Morrison and Boyd, 1967). An example of a center of asymmetry would be an asymmetric carbon atom as in 1-alanine; an example of a molecular unit of asymmetry would be tris (ethylenediamine) chromium (III) ion. The specific optical rotation of substance II is +68 (maximum, table 6) which may be compared with +128 for the poison of *Gymnodinium catenella* (Schantz et al., 1966). The former value was obtained at 546 mμ, and the latter was probably obtained at 589 mμ.

STRUCTURAL FEATURES

A complete structural determination of the toxin(s) was beyond the scope of the present study, but several structural features became apparent. These are valid, of course, for the toxin at the described state of purification.

First, the spectrum of substance I evidently contains a carbonyl group, =C=O; that of substance II does not (fig. 3). Both substances have infrared spectra that are consistent with organophosphates R-PO(OR)$_2$, where R is an oxygenated hydrocarbon moiety.

Second, the toxin molecule contains some asymmetric feature, either an asymmetric carbon atom(s) or a larger asymmetric unit.

Third, some structural features are indicated by the mass spectrum (Beynon, 1960; Biemann, 1962), though the spectrum must be interpreted with some care because of the volatility of substance II. For example, the maximum formula weight of a stable fragment is 508. Any fragments having greater formula weights are too volatile or too short-lived to be detected. It is also possible that the substance readily decomposes into three fragments with similar formulas; thus, the value of 508 corresponds to about one-third of the calculated empirical formula weight.

Finally, it may be hypothesized that a toxin portion of molecular weight 650 decomposes into two fragments with m/e values of about 508 and 147. The latter fragment might be a phosphate ester OP(OR)OR.

Peak assignments, which appear to be reasonable on the basis of available data (table 7), include the following:

1. The peak at m/e=31 probably corresponds to phosphorus-31.
2. The peak at m/e=63 is attributable to a PO_2 unit, which should come from the R′-PO(OR)$_2$ structure.
3. The P(OR)(OR′) fragment might be assigned to the peaks at m/e=138–143. If R and R′ is CH_2CH_3, a m/e value of 137 would be expected; if R is $CH=CH_2$ and R′ is $CH_2CH=CH_2$ m/e value of 142 would be expected. The second possibility is consistent with the ultraviolet absorption spectrum. Cleavage of the vinyl group would account for peaks at about 27 ($CH=CH_2$) and 121 [PO(OCH=CH_2)OCH_2]. Further cleavage of a methylene fragment would account for a peak at about 107.

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[7] The observed value is based on a molecular weight of 650; the calculated value is based on an empirical formula weight of 1545.

of the Gulf Coast Marine Health Sciences Laboratory, Dauphin Island, reviewed this manuscript.

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THE FOOD OF SKIPJACK AND YELLOWFIN TUNAS IN THE ATLANTIC OCEAN[1]

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ABSTRACT

Samples were examined from the stomachs of 1,060 skipjack tuna and 611 yellowfin tuna captured by live bait, longline, trolling, and purse seine in the eastern and western tropical and subtropical Atlantic Ocean in 1965 and 1966. Fish, mollusks, and crustaceans were the principal foods of both species. The major families of fish represented were Scombridae, Carangidae, Serranidae, Balistidae, Gempylidae, and Tetraodontidae; mollusks consisted chiefly of cephalopods (squids); and crustaceans were principally larval macrozooplankton. Frequency of occurrence and displacement volume are given for all taxons of food organisms identified from the stomachs of each species.

Fish was the predominant forage volumetrically throughout the Atlantic Ocean and numerically in the western Atlantic; crustaceans were predominant numerically in tunas caught in the eastern Atlantic. In general, crustaceans predominated in the stomachs of the smaller tunas and fish in the stomachs of the larger ones. When the mean percentages of the three principal sources of tuna food—fish, mollusks, and crustaceans—were compared (for tunas caught concurrently), the evidence was that skipjack tuna ate more crustaceans than did yellowfin tuna. Juvenile tunas were eaten by both skipjack and yellowfin tunas.

This report on the food and feeding habits of skipjack and yellowfin tunas in the Atlantic Ocean is part of an investigation of the ecology of Atlantic tunas carried on at TABL (Tropical Atlantic Biological Laboratory) of BCF (Bureau of Commercial Fisheries). A thorough knowledge of food and feeding habits of tuna is important to an understanding of the biology, abundance, and distribution of tuna species (Reintjes and King, 1953; King and Ikehara, 1956; Iversen, 1962; and Nakamura, 1969).

Atlantic tuna fisheries are sustained in great part by five species considered of worldwide importance: yellowfin tuna (*Thunnus albacares*), skipjack tuna (*Katsuwonus pelamis*), albacore (*T. alalunga*), bigeye tuna (*T. obesus*), and bluefin tuna (*T. thynnus*).

The literature on the food and feeding habits of tunas in the Atlantic Ocean was reviewed by Dragovich (1969). Many publications are available on the feeding habits of the various species of Atlantic tunas, but most of them are based on casual observations involving small samples. Some papers consist of mere taxonomic listings of forage organisms found in tuna stomachs; others contain lists of forage organisms and morphometric measurements; few include quantitative analyses of data, or consideration of the relation of forage organisms to geographic areas, to the size of tunas, or to the habitat.

MATERIALS AND METHODS

Of 1,671 tuna stomachs examined (table 1), about 55 percent were collected on cruises by the research vessels *Geronimo* and *Undaunted* of TABL; 23 percent were supplied to TABL by ORSTOM (Office de la Recherche Scientifique et Technique Outre-Mer), Pointe Noire, Africa; and the rest came from other BCF laboratories and commercial vessels. All data were collected during 1965 and 1966, from three arbitrarily defined areas of the Atlantic Ocean (fig. 1).

In area 1, skipjack tunas were caught by purse seine and yellowfin tunas on longlines; in areas 2 and 3, all tunas were caught at the surface by live bait and trolling.

The fork lengths of the fish measured (figs. 2 and 3) ranged from 22 to 81 cm. for skipjack

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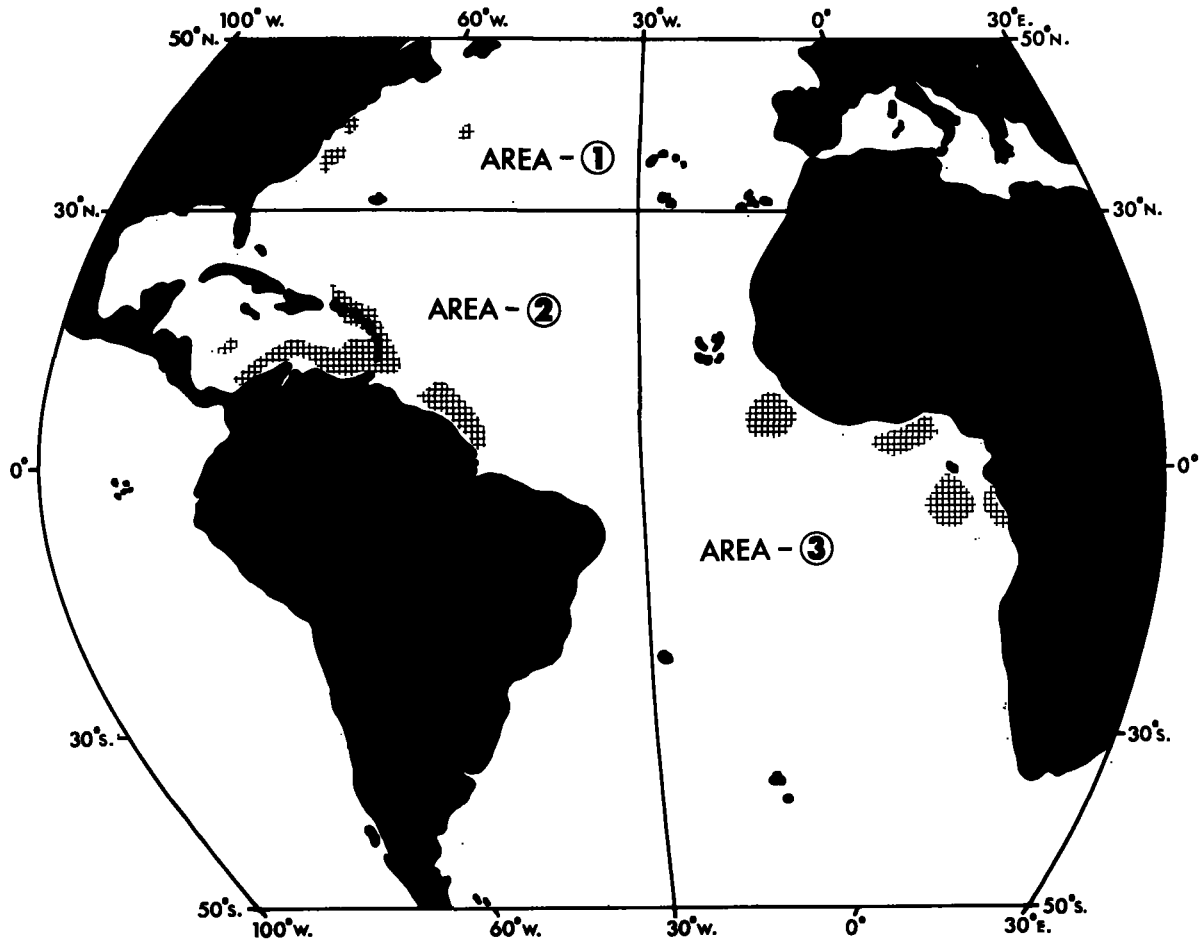

FIGURE 1.—Crosshatching shows localities in areas 1, 2, and 3 where stomachs of skipjack and yellowfin tunas were collected.

tuna and 40 to 155 cm. for yellowfin tuna. (Not all tunas were measured.) Most of the tunas were caught in areas 2 and 3 (table 1).

The interval between capture of fish and removal of stomachs varied considerably, from a few minutes for fish captured by live bait to several hours for some of the fish caught by longline and purse seine. In most collections, each stomach was pierced in several places and then placed in an individual polyethylene bag that contained 10 percent Formalin.[2]

Samples from West African waters were preserved in Formalin and shipped to TABL in sealed metal drums; samples from BCF laboratories or from commercial tuna vessels arrived at TABL either frozen or preserved in Formalin.

At the laboratory, frozen stomachs were thawed and the contents were removed, preserved in 10 percent Formalin, and later sorted. Before forage organisms were sorted and identified, the stomach contents were leached in fresh water for 12 to 24 hours to remove the Formalin. After the food items had been sorted into major groups, they were identified as completely as possible and the number of each taxonomic entity (species or higher taxonomic group) was recorded on data sheets for each stomach. Each taxon was measured volumetrically by the displacement of water in a graduate cylinder of appropriate size. Bait found in the stomachs was not included as food.

[2] Trade names referred to in this paper do not imply endorsement of commercial products by the Bureau of Commercial Fisheries.

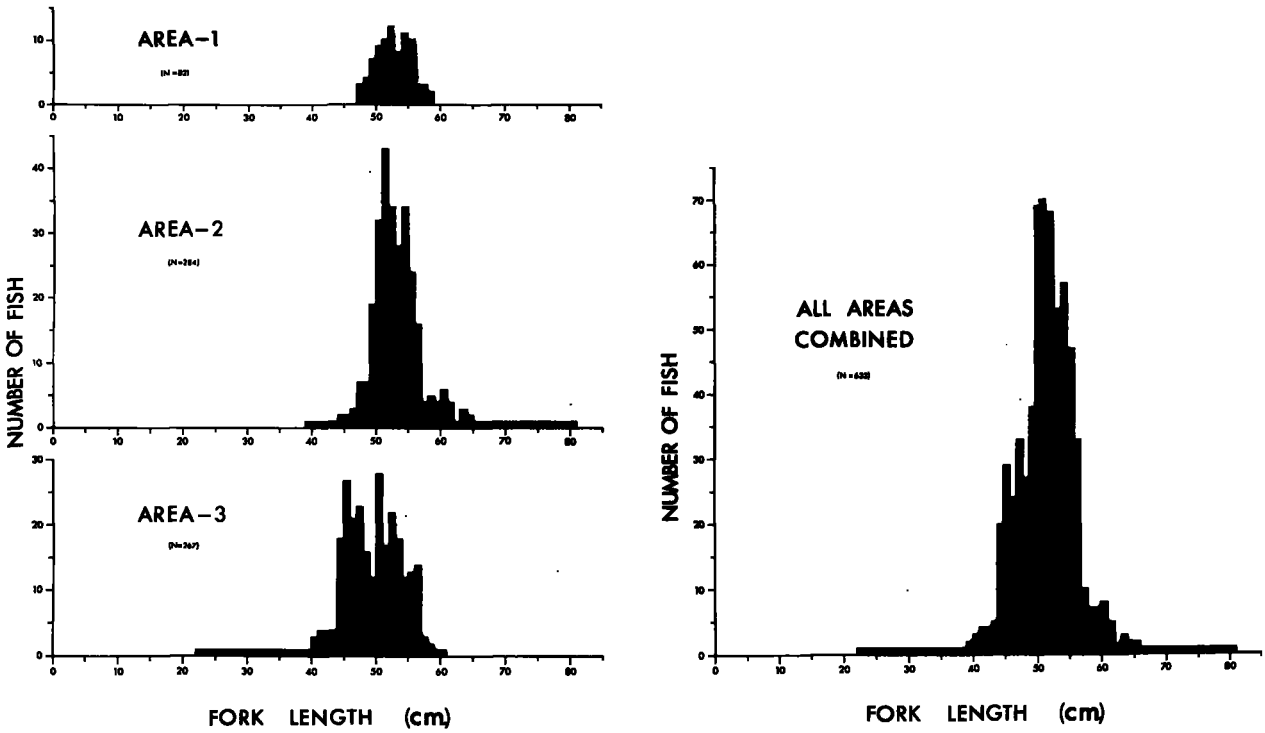

FIGURE 2.—Length-frequency distribution of skipjack tuna from which stomachs were collected.

TABLE 1.—*Tuna stomachs examined from three areas of the Atlantic Ocean*

[See figure 1 for locations of the areas]

Area	Skipjack tuna				Yellowfin tuna			
	Total	With food	Empty		Total	With food	Empty	
	No.	*No.*	*No.*	*Percent*	*No.*	*No.*	*No.*	*Percent*
1	150	82	68	45.3	16	16	0	0
2	389	347	42	10.8	41	39	2	4.9
3	521	257	264	50.7	554	520	34	6.1
Total	1,060	686	374	35.3	611	575	36	5.9

IDENTIFICATION OF TUNA FORAGE ORGANISMS

The identification of tuna forage was complicated by the poor condition of many of the organisms and by the predominance of juvenile or larval forms, for which taxonomic literature is practically nonexistent. Partially digested organisms also were difficult to identify. The organisms that lacked external protective devices (such as the scales of fish or the exoskeletons of crustaceans) were digested most rapidly and were, therefore, the most difficult to identify. Cephalopods, for instance, presented difficulties because they are identified primarily on the basis of skin, suckers, and fins. Squids were separated from octopuses on the basis of number of arms (10 in squid and 8 in octopus), lack of a gladius ("pens," or internal skeleton) in the octopus, and the shape of the beaks. Ommastrephid squids were identified by the inverted T-shaped funnel (known as the locking apparatus), which distinguishes this family from all others, even in the youngest stages.

The shelled mollusks, heteropods, pteropods, and nautiloid cephalopods were identified from their shell remains. Exoskeletons provided diagnostic characters for identification of arthropods.

The crustaceans were identified mostly on the basis of their remaining exoskeletons. Larvae of crustaceans were sorted into zoea and megalopae or their equivalent stages, and then identified as far as was possible.

Identification of fish was troublesome because their best diagnostic features (scales, fins) are external and are the first to be digested. Partly digested teleost fishes that lacked external characters were identified from skeletal remains. Other characters used were scutes, dorsal spines, gill rakers, photophores, teeth, and body shape.

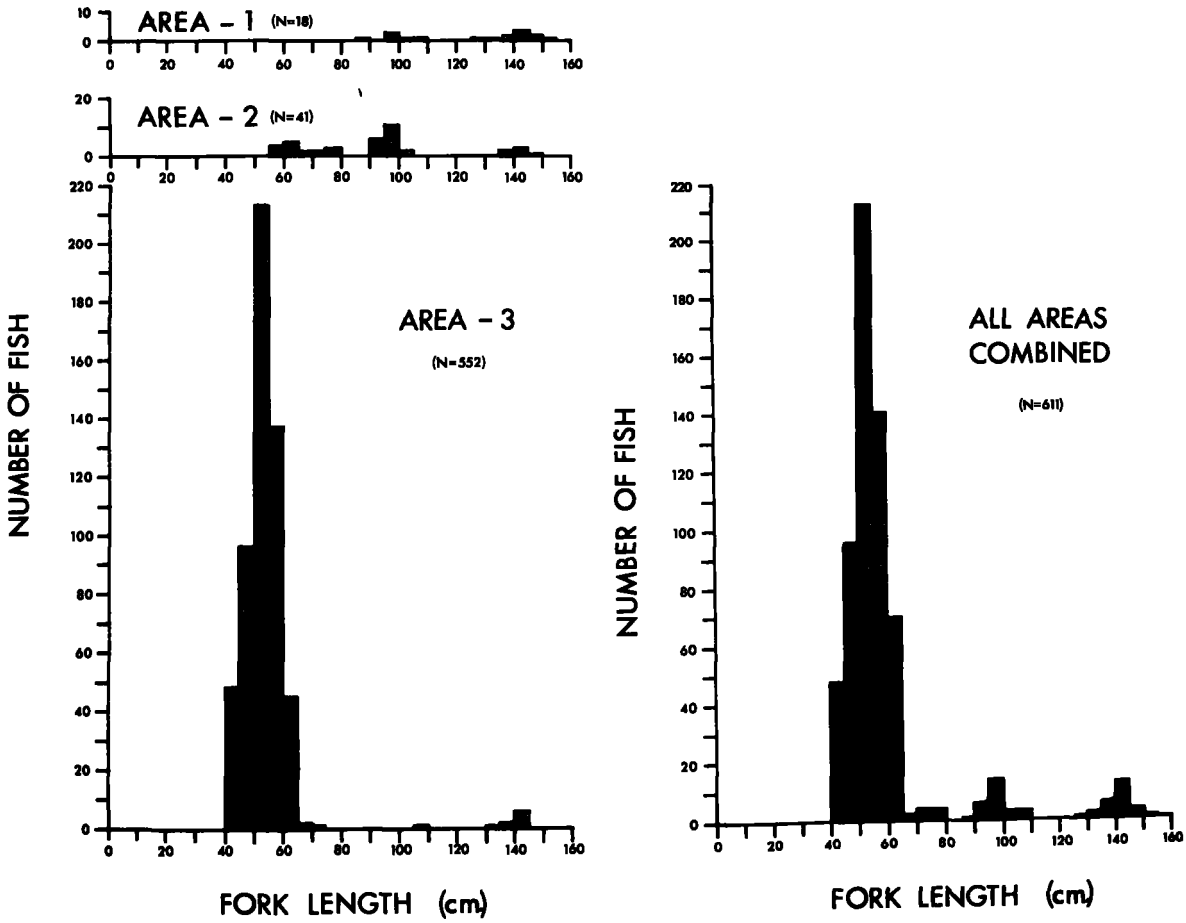

FIGURE 3.—Length-frequency distribution of yellowfin tuna from which stomachs were collected.

METHODS USED IN THE EVALUATION OF DATA

The data were evaluated by percentage frequency of occurrence and percentage of total volume (Reintjes and King, 1953). Statistical analyses were based on Spearman's rank correlation test and a paired t-test of difference between means.

COMPOSITION OF FORAGE ORGANISMS FOUND IN THE STOMACHS OF SKIPJACK AND YELLOWFIN TUNAS

The identified food of skipjack and yellowfin tunas consisted chiefly of three major categories—fish, crustaceans, and cephalopods (fig. 4). Appendix tables 1 to 6 list all individual food items identified from stomachs of skipjack and yellowfin tunas. These tables include for each area the food item, the number of stomachs in which it occurred, the percentage frequency of occurrence, the displaced volume, and the percentage of the total volume examined. The food items are listed in order of frequency of occurrence by families (fishes) or broader categories (mollusks and crustaceans).

The numbers of taxa found in the stomachs of the two species were similar—159 in skipjack tuna and 174 in yellowfin tuna; 102 were in stomachs of both species (59 fishes, 29 crustaceans, and 14 mollusks).

The taxonomic composition of forage organisms differed in the three areas. In areas 1 and 2, fish was the most important food item in volume and frequency of occurrence for both species (fig. 4). In area 3, crustaceans led fish and mollusks in frequency of occurrence for both species; by volume, crustaceans were more important than fish only in the diet of skipjack tuna. Cephalopods (chiefly squid) made up the major portion of mollusks in all areas; by volume, cephalopods were more important than

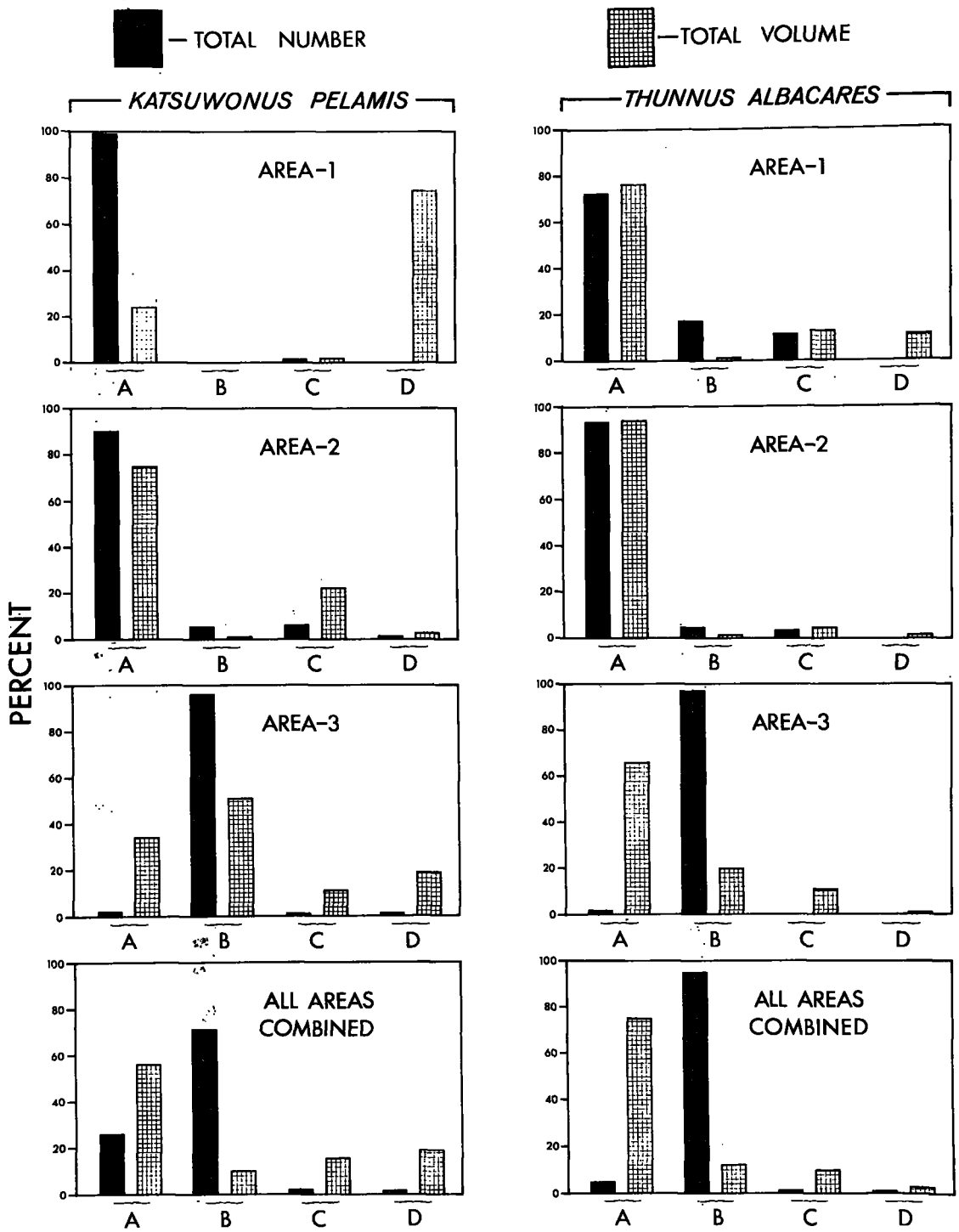

FIGURE 4.—Percentage of total food (by four major categories) in stomachs of skipjack and yellowfin tunas captured in various sections of the Atlantic Ocean. Solid columns represent the number of organisms and checkered columns represent volumes. A=fishes; B=crustaceans; C=cephalopods; D=other mollusks and unidentifiable.

crustaceans in areas 1 and 2, but less important than crustaceans in area 3. Animals other than fish, crustaceans, and mollusks—heteropods, pteropods, larval Tonnidae, and tunicates—amounted to less than 0.8 percent of the total volume of food in both species. Unidentifiable material consisted of semidigested masses of various food, some of which was recognizable as mollusks other than cephalopods. The percentage volume of unrecognizable material was low for both species in areas 2 and 3 but was extremely high—much higher than that for any other category of food—in skipjack tunas from area 1 (fig. 4).

FISHES

Forage fish consumed by skipjack and yellowfin tunas in all areas consisted primarily of juvenile and larval forms of pelagic fish.

In area 1 (appendix tables 1 and 2) the fish consumed by the two species differed. The forage of skipjack tuna was made up of scombrids (*Scomber* spp. and *Scomber scombrus*) and unidentifiable fish, whereas that of yellowfin tuna included fish from at least 15 families.

In areas 2 and 3, the food of skipjack and yellowfin tunas was similar (appendix tables 3–6). In area 2 (appendix tables 3 and 4), 29 fish families were recorded for skipjack tuna and 23 for yellowfin tuna; 19 were common to the two species. A wide variety of forage fishes was found in tunas from area 2, but only a few taxa ranked high in frequency of occurrence and volume for both species. Large numbers of *Paranthias furcifer, Dactilopterus volitans,* and *Holocanthus* spp. were present—the stomach of one yellowfin tuna contained 710 specimens of *P. furcifer*. In area 3 (appendix tables 5 and 6), 38 forage fish families were recorded for yellowfin tuna and 21 for skipjack tuna; 20 fish families were common to both.

Among the families of forage fishes, in frequency of occurrence and by volume, Scombridae constituted the most important food of skipjack and yellowfin tunas in area 1, and also of skipjack tuna in area 2 (appendix tables 1–6). Serranidae occurred most frequently in the diet of yellowfin tuna in area 2, and also ranked high as forage of skipjack tuna. Other fish in area 2 that ranked high in frequency of occurrence and by volume for both tunas were Scombridae, Carangidae, Dactylopteridae, and Chaetodontidae.

In area 3, Carangidae, Tetraodontidae, Gempylidae, and Serranidae were the most numerous forage fishes of yellowfin tuna; they also ranked high in frequency of occurrence and by volume in the diet of skipjack tuna.

CRUSTACEANS

Crustaceans in stomachs of skipjack and yellowfin tuna consisted of a wide variety of forms. Larval macrozooplanktonic forms, which made up the bulk of crustaceans in all areas, were different types of zoea, megalopae, or their equivalent stages. Amphipods (hyperiids), *Heterocarpus ensifer,* mysids, and euphausiids also were present but of less consequence.

Individual taxa of crustaceans contributed little to the total volume of forage organisms. Collectively—because of their substantial numbers and high frequency of occurrence—crustaceans were important in the forage of skipjack and yellowfin tunas in area 3, where counts of crustaceans exceeded those of fish (fig. 4). In frequency of occurrence but not in volume, crustaceans exceeded fish in the diet of yellowfin tuna in area 3. Crustaceans in the diets of tunas in area 3 consisted of 34 taxa for skipjack tuna and 39 taxa for yellowfin tuna; 25 taxa were common to both species (appendix tables 5 and 6). The chief constituents (frequency of occurrence and by volume) in the crustacean diet of the two species of tuna in area 3 were larval stomatopods, and megalopal stages listed as Decapoda (Brachyura) and hyperiid amphipods. Although many amphipods were present in the samples, they consisted of relatively few species. *Phrosina semilunata* was numerically the most important species by far in the diet of both species of tuna. *Heterocarpus ensifer* was the prominent shrimp in the diet of yellowfin tuna; hermit crab larvae (*Petrochirus pustulatus, Dardanus* spp., *D. arrosor,* and *D. pectinatus)* and various phyllosoma stages of *Scyllarus* sp. and *Panulirus rissoni* were important in the diet of both species in area 3 (appendix tables 5 and 6). In area 1, crustaceans found in the stomachs of only yellowfin tunas (appendix table 2) consisted of hyperiid amphipods and megalopal

stages of Brachyura; one group of megalopae, Raninidae, was identified to family. In area 2, megalopal forms—Decapoda (Brachyura) and larval stomatopods—ranked high in frequency of occurrence. Mysis stages of *Cerataspis petiti* were present in the diet of yellowfin tunas in area 2 only (*C. petiti* has never before been reported from the Caribbean Sea).

MOLLUSKS

Numbers of identified mollusks were considerably fewer than those of fishes and crustaceans. Squids (Ommastrephidae) were most numerous in the diet of both species of tunas in all areas (appendix tables 1–6). *Illex illecebrosus* and *Ommastrephes* spp. were the only identified ommastrephids. Pelagic juvenile octopuses were present in the stomachs of both species of tunas. The identified octopods, *Tremoctopus violaceus,* were observed in area 2 (appendix tables 3 and 4).

OTHER FOOD

Heteropods and pteropods were prominent in frequency of occurrence for both species of tuna, but were unimportant volumetrically. The two groups of mollusks were present in the stomachs of skipjack tuna in areas 2 and 3 (appendix tables 3 and 5) and in yellowfin tuna in area 3 (appendix table 6). By frequency of occurrence and volume, heteropods and pteropods were more important in the diet of skipjack tuna than in that of yellowfin tuna in all areas. *Oxygyrus keraudreni, Cavolinia unicinata,* and *Diacria trispinosa* were identified from area 2; *O. keraudreni* was the heteropod found most frequently in both species of tunas in area 3.

Larval Tonnidae (including *Tona galea*) were present in the stomachs of skipjack tuna in area 2 only.

JUVENILE TUNAS AS FOOD FOR SKIPJACK AND YELLOWFIN TUNAS

Information on the distribution and occurrence of juvenile tunas is of great value in identifying the spawning areas of tunas, but the collection of juvenile tunas by standard means is difficult. Tunas themselves, however, are excellent collectors of many marine species, including other tunas. Juvenile tunas were present in all three areas (table 2). All tunas found in the stomachs of skipjack and yellowfin tunas in this study were juveniles; most were identified from vertebrae.

As many as 13 juvenile tunas were found in the stomach of a skipjack tuna, and as many as 24 in the stomach of a yellowfin tuna. *Auxis* spp. (436 specimens, 23–134 mm. long) were the most numerous scombrid in the stomachs of both tuna species (unidentified Scombridae were the only other form recorded for both); *Euthynnus alletteratus* (40–42 mm. long), *Katsuwonus pelamis* (46–94 mm. long), *Thunnus* spp. (64–72 mm. long), and *T. atlanticus* (59 mm. long) were present in the stomachs of skipjack tuna only (one to three specimens per stomach); juvenile *Scomber japonicus* (83–222 mm. long) were present in the stomachs of yellowfin tunas only (one to four per stomach).

TABLE 2.—*Occurrence of juvenile scombrids in the stomachs of skipjack and yellowfin tunas in areas 1, 2, and 3*

[For the areas see figure 1]

	Area 1		Area 2		Area 3	
	Skipjack	Yellowfin	Skipjack	Yellowfin	Skipjack	Yellowfin
Scomber spp.	+			+		
Scomber japonicus						+
Scomber scombrus	+					
Other Scombridae	+		+	+	+	+
Scombroidei						+
Auxis spp.			+	+	+	+
Katsuwonus pelamis			+			
Euthynnus alletteratus			+		+	
Thunnus spp.			+			
Thunnus atlanticus			+			

That juvenile tunas are a part of the diet of adult tunas has been reported often. King and Ikehara (1956) found juvenile skipjack tuna in the stomachs of yellowfin and bigeye tunas; Nakamura (1965) reported a high frequency of occurrence (24.8–44.8 percent) of juvenile tunas in the stomachs of skipjack tunas; Suarez-Caabro and Duarte-Bello (1961) observed juvenile blackfin tunas (5–150 mm., fork length) and skipjack tunas (35–145 mm., fork length) in the stomachs of skipjack tunas; Reintjes and King (1953) found skipjack tuna and various other tuna species in the stomachs of yellowfin tuna; and Koga (1958a, b) and Alverson (1963) reported juvenile tuna in the stomachs of other tunas.

STOMACH CONTENTS OF FISHES INGESTED BY SKIPJACK AND YELLOWFIN TUNAS

Stomach contents of fishes ingested by skipjack and yellowfin tunas were examined to learn more about the food chain of yellowfin and skipjack tuna and the trophic dependence of ingested fishes. The results of this examination, as in the study by Nakamura (1965), further confirmed the dependence of forage fishes upon macrozooplankton. The stomach contents of fishes ingested by both species of tunas consisted primarily of crustaceans and fish remains, but some of the larger fishes contained remains of squid and juvenile fishes. A *Scomber japonicus* from the stomach of a yellowfin tuna collected off West Africa held three juvenile *Sardinella rouxi* (50–60 mm. fork length).

Because crustaceans were better preserved than fishes, I could distinguish broad taxonomic categories. Although I made no quantitative estimates, copepods appeared to be the dominant single group in the diet of most of the ingested fishes. As many as 60 to 100 were found in a single stomach. Among identifiable copepods from the western Atlantic, *Centropages typicus, Temora turbinata,* and other calanoids were most numerous; *Scolecithrix danae, Megacalanus princeps, Scolecithricella* sp. and other calanoids were most numerous in samples taken off the coast of Africa. Other identifiable crustaceans were: amphipods, euphausiids, shrimp, *Lucifer* sp., larval stomatopods, megalopal stages of Raninidae, and megalopal and zoeal stages of Brachyura.

VARIATION IN FOOD IN RELATION TO DISTANCE FROM LAND, TIME OF DAY, AND SIZE OF TUNA

Stomach contents of tunas collected at all locations were classified according to the distance from the nearest land. The arbitrary scale (0–24 nautical miles or 0–43.2 km., 25–49 nautical miles or 45.0–88.2 km., 50–74 nautical miles or 90.0–133.2 km., 100–149 nautical miles or 180.0–268.2 km., 150–200 nautical miles or 270.0–360.8 km., 201–300 nautical miles or 361.8–540.0 km., 301–400 nautical miles or 541.8–720.0 km. and 401 nautical miles or 721.8 km. plus) used in this study to delineate distances from land is the same as that used by King and Ikehara (1956). The mean volumes of 12 taxa most frequently identified as tuna forage from the stomachs of skipjack and yellowfin tuna were plotted for each area and distance. For most of the distances, however, the number of tuna stomachs was too small to warrant any conclusions.

Data were insufficient for analyses of monthly or seasonal variations, and the trend of feeding throughout the day could be considered only for skipjack tuna from areas 2 and 3. Average volumes of stomach contents were calculated for each hour of the day. The percentage of empty stomachs appeared highest, and the mean volume of food in stomachs lowest, near midday. A chi-square test of heterogeneity (Snedecor and Cochran, 1967: 248) indicated that the observed differences in percentage of empty stomachs near midday was significant ($P<0.005$) in areas 2 and 3.

The diurnal fluctuation in feeding was similar to that observed by other investigators (Talbot and Penrith, 1963; Nakamura, 1965; and Sokolov, 1967). Nakamura (1965) suggested that the diurnal feeding pattern of skipjack tuna was based on availability of food (movement of zooplankton and forage organisms, during the midday period of maximum illumination, to depths beyond those occupied by the surface-dwelling skipjack tuna) or to satiation of tuna after the morning feeding period.

The relation between the sizes of skipjack and yellowfin tunas and the taxonomic composition of food was studied in terms of frequency of occurrence and percentage volume of the three principal food categories (fishes, mollusks, and crustaceans). The occurrence of crustaceans tended to decline as the size of skipjack tunas increased; the frequency of occurrence of fish increased with the size of tunas of both species. I observed no relation between the size of tunas and the consumption of cephalopods and other mollusks.

Spearman's rank correlation analysis (Steel and Torrie, 1960: 409) was used to determine whether the frequency of occurrence of the two

dominant forage food items (fish and crustaceans) in the stomachs of skipjack tunas was correlated with the size of tunas. Spearman's rank correlation coefficients of 0.771 for fish and –0.771 for crustaceans were not significant. I did not make a similar analysis of the sizes of yellowfin tunas and the frequency of occurrence of the three main food categories because the number of size classes (four) was too small.

Spearman's rank correlation analysis was also applied to test whether the percentage volumes of the forage food categories of skipjack and yellowfin tunas were correlated with the size of fish (table 3). All fish suitable for such a test (487 skipjack and 338 yellowfin tunas) were grouped into 10-mm. length intervals. Correlations were performed for the two dominant food categories (fish and crustaceans or mollusks). The data from single cruises were treated separately, because each cruise is representative of the same general area and the same time. I observed a significant correlation (Spearman's rank correlation coefficient of 0.512, $P \leq 0.05$) only between yellowfin tuna and fish on one cruise, indicating that as the size of tuna increased, the percentage consumption of volume of forage fish increased also.

The size ranges of skipjack (410–639 mm. fork length) and yellowfin tunas (390–629 mm. fork length) were for the most part probably not great enough to relate possible differences in feeding habits to size. Even so, the fact that one significant correlation was noted for yellowfin tuna may indicate that larger tunas consume more fishes than do the smaller ones. The greater dependence of larger skipjack and yellowfin tunas on fish and of smaller skipjack tuna on crustaceans was also observed by other investigators (Nakamura, 1965; Yuen, 1959; and Alverson, 1963).

TABLE 3.—*Spearman's coefficients of rank correlation (r_s) between the lengths of skipjack and yellowfin tunas and percent volumes of the dominant food categories for several cruises*

Cruise	Tuna species	Tuna examined	Fork length	Fish (r_s)	Crustaceans (r_s)	Mollusks (r_s)
		No.	*Mm.*			
Geronimo 7	Skipjack	12	460–579	0.077	----	0.107
Geronimo 5	do	17	410–579	.128	0.127	----
Do	Yellowfin	18	390–569	.512	----	–.337
Kuroshio Maru	do	19	410–629	.004	.132	----
Do	Skipjack	16	410–569	.087	.192	----
Undaunted 2	do	22	397–639	.150	----	.219

King and Ikehara (1956), who analyzed the relation between the volume of stomach contents and body weights for bigeye and yellowfin tunas from the central Pacific, found that the mean volume per stomach for both species increased with the size of the fish and the average content of stomachs per unit of body weight decreased with increase in size. Because about 98 percent of the specimens I studied fell into a narrow range of sizes (2–4 kg.), I was unable to make a similar analysis, but I did find—from examinations of scatter diagrams—that the relation between the volume of the stomach contents and the weight of the fish appeared to agree with King and Ikehara's results.

VARIATION IN VOLUME OF STOMACH CONTENTS

As indicated in the studies by Magnuson (1969), the maximum capacity of the stomach of a skipjack tuna is about 7 percent of the weight of the fish, but during 1 day a fish can consume the equivalent of 15 percent of its body weight. On the basis of Magnuson's study, I assume that the maximum capacity of yellowfin tuna stomachs is also about 7 percent of the body weight.

The volume of stomach contents was less than 20 ml. in 75 percent of the skipjack tunas and in 85 percent of the yellowfin tunas. Stomach volumes above 20 ml. were higher in areas 1 and 2 than in area 3—an observation that might be related to the fact that the diet of skipjack and yellowfin tunas in areas 1 and 2 consisted primarily of fish, which have higher average volumes than crustaceans. In their study of food of yellowfin tuna in the central Pacific, Reintjes and King (1953) found that food volume was less than 25 cc. in 58 percent of the stomachs of yellowfin tunas. Assuming that 1.0 ml. of stomach contents is equivalent to 1.0 g., I made a rough comparison between the estimated weight of the stomach contents and the body weight of tunas. My calculations showed that in 99 percent of the observations the stomach contents were well

below the maximum capacity (7 percent of body weight) shown by Magnuson. Thus, my figure of 20 ml. probably does not represent the average daily ration for either species, particularly because the volumes were as high as 149 ml. in skipjack tuna and 499 ml. in yellowfin tuna. The fact that less than 20 ml. of food was found in most stomachs I examined (both species) also may suggest that (1) food is not always available and (2) the rates of digestion are rapid.

COMPARISON OF FOOD OF SKIPJACK TUNA AND YELLOWFIN TUNA

When data from all areas are combined, the large number of forage taxa common to skipjack and yellowfin tunas indicates a marked similarity in the diets of the two species. When the taxonomic composition of the food in stomachs of the two species was compared at locations where they were caught simultaneously, however, less than half of the total taxa at 23 of 25 stations were common to both species—suggesting that feeding is selective. Crustaceans made up the greatest number of taxa common to both species, and fishes the least (fig. 5).

Consideration of feeding selectivity of skipjack and yellowfin tunas required that the data be examined quantitatively. The percentage volume for each food category (fish, mollusks, and crustaceans) and for each station was transformed by $Y = \text{arc-sin } \sqrt{x}$, where x is the fraction of the volume and y the transformed variate upon which the Spearman's coefficient of rank correlation was applied to see if the volume of fish among food constituents varied directly or inversely between the skipjack and yellowfin tunas. I found that the rank correlation coefficient of 0.241 was not significant. A comparison (paired *t*-test) of the mean percentages of the three main food categories (fish, crustaceans, and mollusks) at the same stations gave evidence that the mean percentage of crustaceans in the stomachs was greater in skipjack tuna than in yellowfin tuna ($P \leq 0.01$).

Findings by other investigators concerning selectivity in feeding by different species of tunas varied. Among fish from the same locations in the Pacific, Iversen (1962) found that the food of albacore was more similar to that of yellowfin tuna than to that of bigeye tuna—even though bigeye tuna and albacore inhabit deeper water than yellowfin tuna. Some selectivity in feeding might be inferred from Iversen's study. King and Ikehara (1956) studied the food of bigeye and yellowfin tunas in the central Pacific and concluded that their forage was, in general, remarkably similar. They stated that when the two species live in the same area, food habits are alike, and that food selectivity is probably attributable to a movement by the tunas to different feeding areas.

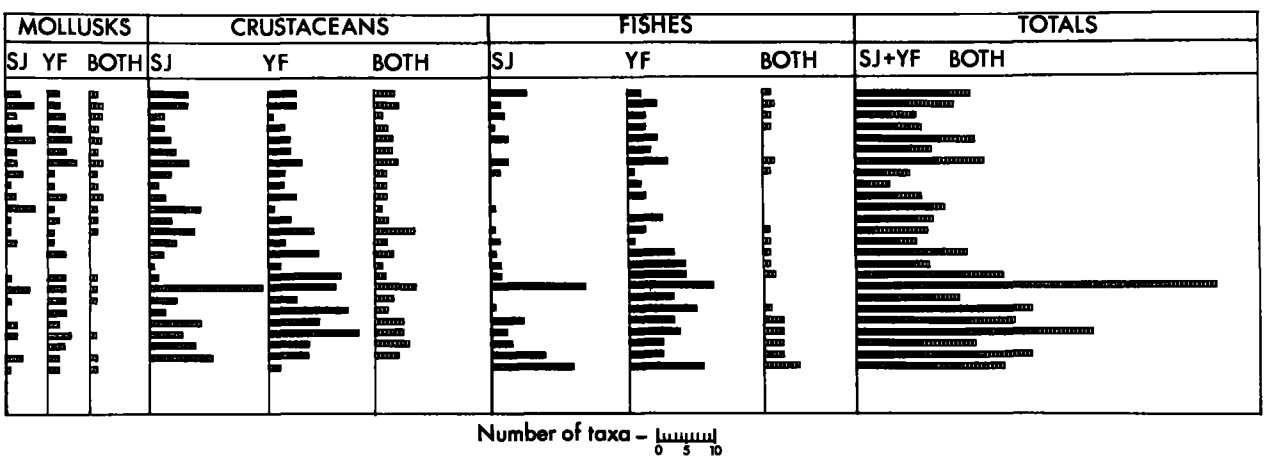

FIGURE 5.—Number of different forage taxa from the stomachs of SJ (skipjack tuna) and YF (yellowfin tuna), collected simultaneously at the same stations.

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APPENDIX

TABLE 1.—*List of forage organisms (arranged in order of frequency of occurrence) found in 82 skipjack tuna stomachs with food, collected from area 1*

[Frequency of occurrence and volume are given for each taxon. See figure 1 for location of area of sampling]

Taxon	Frequency of occurrence		Volume	
	No.	Per-cent	Ml.	Per-cent
Fishes:				
Unidentifiable	6	7.2	7.0	1.2
Scombridae:				
Scomber spp.	46	56.0	135.1	24.0
Scomber sombrus	35	42.6	373.2	66.3
Other Scombridae	3	3.6	6.6	1.2
Mollusks:				
Ommastrephidae	3	3.6	40.9	7.3

TABLE 2.—*List of forage organisms (arranged in order of frequency of occurrence) found in 16 yellowfin tuna stomachs with food, collected from area 1*

[Frequency of occurrence and volume are given for each taxon. See figure 1 for location of area of sampling]

Taxon	Frequency of occurrence		Volume	
	No.	Per-cent	Ml.	Per-cent
Fishes:				
Unidentifiable	14	87.5	257.2	21.8
Bramidae				
Collybus drachme	5	31.2	42.7	3.6
Brama rayi	1	6.2	3.9	0.3
Pterycombus goodei	1	6.2	3.0	0.2
Balistidae				
Balistes spp.	2	12.5	19.7	1.7
Other Balistidae	3	18.7	13.8	1.2
Gempylidae				
Gempylus serpens	4	25.0	62.0	5.2
Other Gempylidae	2	12.5	7.6	0.6
Dactylopteridae				
Dactylopterus volitans	5	31.2	23.7	2.0
Holocentridae				
Holocentrus spp.	3	18.7	19.3	1.6
Holocentrus vexillarius	1	6.2	9.2	0.8
Scombridae				
Auxis spp.	4	24.9	314.8	26.6
Triglidae				
Peristedion spp.	2	12.5	3.3	0.3
Monocanthidae				
Cantherines sp.	2	12.5	4.2	0.4
Exocoetidae	1	6.2	8.5	0.7
Belonidae	1	6.2	31.0	2.6
Syngnathidae				
Hippocampus spp.	1	6.2	1.0	0.1
Branchiostegidae				
Malacanthus sp.	1	6.2	4.6	0.4
Coryphaenidae				
Coryphaena spp.	1	6.2	94.0	8.0
Coryphaena hippurus	1	6.2	75.0	6.4
Acanthuridae				
Acanthurus spp.	1	6.2	3.9	0.3
Other Acanthuridae	1	6.2	0.2	<0.1
Molidae				
Mola mola	1	6.2	1.2	0.1
Mollusks:				
Cephalopoda				
Octopoda				
Argonauta sp.	1	6.2	23.5	2.0
Teuthoidea				
Unidentified				
Ommastrephidae	3	18.7	34.5	2.9
Unidentified Teuthoidea	5	31.2	106.0	9.0
Other Cephalopoda	2	12.5	0.2	<0.1

TABLE 2.—*List of forage organisms (arranged in order of frequency of occurrence) found in 16 yellowfin tuna stomachs with food, collected from area 1*—Continued

Taxon	Frequency of occurrence		Volume	
	No.	Per-cent	Ml.	Per-cent
Gastropoda				
Helisoma dury	1	6.2	0.3	<0.1
Crustaceans:				
Decapoda				
Brachyura (megalopae)	1	6.2	0.1	<0.1
Raninidae (megalopae)	1	6.2	0.8	<0.1
Amphipoda (Hyperiidae)				
Phrosina semilunata	3	18.7	11.3	1.0
Phronima sedentaria	1	6.2	0.2	<0.1
Brachyscelus spp.	1	6.2	0.5	<0.1
Other Hyperiidea	1	6.2	0.5	<0.1

TABLE 3.—*List of forage organisms (arranged in order of frequency of occurrence) found in 347 skipjack tuna stomachs with food, collected from area 2*

[Frequency of occurrence and volume are given for each taxon. See figure 1 for location of area of sampling]

Taxon	Frequency of occurrence		Volume	
	No.	Per-cent	Ml.	Per-cent
Fishes:				
Unidentifiable	241	69.4	895.9	16.9
Scombridae				
Auxis spp.	85	24.5	680.8	12.9
Katsuwonus pelamis	10	2.9	86.0	1.6
Euthynnus alletteratus	1	0.3	0.3	<0.1
Thunnus spp.	3	0.8	9.6	0.2
Thunnus atlanticus	1	0.3	2.0	<0.1
Other Scombridae	89	25.6	269.9	5.1
Gempylidae				
Gempylus sp.	1	0.3	0.9	<0.1
Gempylus serpens	40	11.5	103.2	1.9
Nesiarchus nasutus	2	0.5	11.7	0.2
Other Gempylidae	52	14.9	72.1	1.4
Chaetodontidae				
Holacanthus spp.	58	16.7	50.2	0.9
Holacanthus tricolor	2	0.5	0.5	<0.1
Holacanthus ciliaris	2	0.5	0.7	<0.1
Chaetodon sedentarius	1	0.3	0.1	<0.1
Chaetodon spp.	30	8.6	18.4	0.3
Mullidae				
Pseudupeneus spp.	1	0.3	8.8	0.2
Pseudupeneus maculatus	19	5.5	174.2	3.3
Other Mullidae	67	19.3	390.7	7.4
Serranidae				
Paranthias sp.	1	0.3	0.2	<0.1
Paranthias furcifer	75	21.6	440.1	8.3
Other Serranidae	4	1.1	2.0	<0.1
Acanthuridae				
Acanthurus spp.	55	15.8	71.7	1.4
Acanthurus coeruleus	18	5.2	21.6	0.4
Acanthurus bahianus	1	0.3	2.2	<0.1
Holocentridae				
Holocentrus spp.	61	17.6	58.5	1.1
Holocentrus vexillarius	4	1.1	2.2	<0.1
Myripristis jacobus	1	0.3	3.0	<0.1
Other Holocentridae	3	0.8	0.6	<0.1
Dactylopteridae				
Dactylopterus volitans	66	19.0	110.9	2.1
Monacanthidae				
Monacanthus spp.	13	3.7	5.8	0.1
Cantherines sp.	20	5.8	34.6	0.6
Cantherines pullus	1	0.3	9.0	0.2
Alutera spp.	1	0.3	0.2	<0.1
Other Monacanthidae	39	11.2	35.7	0.7
Carangidae				
Vomer setapinnis	22	6.3	26.1	0.5
Decapterus spp.	4	1.1	12.5	0.2
Decapterus punctatus	5	1.4	31.4	0.6
Caranx spp.	5	1.4		
Caranx bartholomaei	3	0.8	3.4	<0.1
Trachinotus spp.	2	0.5	0.9	<0.1

TABLE 3.—*List of forage organisms (arranged in order of frequency of occurrence) found in 347 skipjack tuna stomachs with food, collected from area 2*—Continued

Taxon	Frequency of occurrence		Volume	
	No.	Percent	Ml.	Percent
Selar sp.	1	0.3	4.0	<0.1
Selar crumenopthalmus	2	0.5	3.0	<0.1
Other Carangidae	16	4.6	105.9	2.0
Balistidae				
Balistes spp.	17	4.9	78.8	1.5
Balistes vetula	4	1.1	76.5	1.4
Xanthichthys ringens	1	0.3	3.0	<0.1
Other Balistidae	10	2.9	9.1	0.2
Stromateidae				
Cubiceps spp.	20	5.8	128.0	2.4
Cubiceps gracilis	1	0.3	1.3	<0.1
Other Stromateidae	3	0.8	8.6	0.2
Tetraodontidae				
Sphaeroides spp.	8	2.3	6.3	0.1
Lagocephalus spp.	5	1.4	7.4	0.1
Lagocephalus pachycephalus	1	0.3	2.2	<0.1
Other Tetraodontidae	9	2.6	6.5	0.1
Priacanthidae				
Priacanthus spp.	6	1.7	9.6	0.2
Priacanthus crucnatus	2	0.5	2.0	<0.1
Priacanthus arenatus	1	0.3	1.0	<0.1
Pseudopriacanthus altus	4	1.1	4.7	0.1
Other Priacanthidae	9	2.6	9.1	0.2
Syngnathidae				
Syngnathus spp.	10	2.9	1.0	<0.1
Syngnathus floridae	2	0.5	0.3	<0.1
Hippocampus spp.	1	0.3	0.1	<0.1
Hippocampus erectus	2	0.5	0.7	<0.1
Other Syngnathidae	1	0.3	0.1	<0.1
Scorpaenidae				
Scorpaena spp.	10	2.9	1.8	<0.1
Other Scorpaenidae	5	1.4	0.6	<0.1
Ostraciidae				
Lactophrys spp.	10	2.9	2.3	<0.1
Exocoetidae				
Exocoetus obtusirostris	1	0.3	50.0	0.9
Hirundichthys sp.	1	0.3	0.9	<0.1
Other Exocoetidae	7	2.0	64.1	1.2
Congridae	7	2.0	2.2	0.1
Percoidei	7	2.0	7.1	<0.1
Molidae				
Ranzania laevis	3	0.8	9.2	0.2
Other Molidae	1	0.3	0.6	<0.1
Bramidae				
Collybus drachme	4	1.1	2.5	<0.1
Scombroidei	4	1.1	4.0	0.1
Anguilloidei	3	0.8	0.8	<0.1
Coryphaenidae				
Coryphaena spp.	1	0.3	1.5	<0.1
Balistoidei	1	0.3	0.3	<0.1
Diodontidae	1	0.3	0.2	0.1
Paralepididae	1	0.3	0.8	0.1
Branchiostegidae				
Malacanthus plumieri	1	0.3	1.5	<0.1
Chiasmodontidae	1	0.3	0.6	<0.1
Caproidae				
Antigonia capros	1	0.3	0.6	<0.1
Ophichthidae	1	0.3	0.6	<0.1
Polynemidae	1	0.3	16.5	0.3
Mollusks:				
Cephalopoda				
Octopoda				
Tremoctopus violaceus	1	0.3	0.5	<0.1
Unidentified Octopoda	2	0.6	0.3	<0.1
Teuthoidea				
Unidentified Ommastrephidae	63	18.2	439.1	8.3
Illex illecebrosus	28	8.1	321.6	6.1
Ommastrephes spp.	1	0.3	8.0	0.2
Teuthoidea	4	1.2	5.6	<0.1
Other Cephalopoda	33	9.5	205.7	3.9
Gastropoda				
Heteropoda				
Oxygyrus keraudreni	6	1.7	0.6	0.1
Atlantidae	1	0.3	0.1	<0.1
Pteropoda				
Cavolinia uncinata	8	2.3	1.0	<0.1
Diacria trispinosa	1	0.3	0.1	<0.1
Tonnidae (larval forms)				
Tonna galea	1	0.3	0.1	<0.1
Other Tonnidae	1	0.3	0.1	<0.1

TABLE 3.—*List of forage organisms (arranged in order of frequency of occurrence) found in 347 skipjack tuna stomachs with food, collected from area 2*—Continued

Taxon	Frequency of occurrence		Volume	
	No.	Percent	Ml.	Percent
Crustaceans:				
Decapoda				
Brachyura (megalopae)	30	8.6	3.6	0.1
Unidentified Raninidae (megalopae)	22	6.3	3.4	0.1
Macrura-Natantia				
Caridea (larvae)	2	0.6	1.1	<0.1
Macrura-Reptantia				
Unidentified (Phyllosomae)	1	0.3	0.1	<0.1
Stomatopoda				
Unidentified Stomatopoda (larval forms)	27	7.8	11.4	0.2
Amphipoda (Hiperiidea)				
Phronima sedentaria	1	0.3	0.2	<0.1
Other Hyperiidea	4	1.2	0.4	<0.1
Isopoda	2	0.6	0.2	<0.1
Other crustaceans	17	4.9	2.2	<0.1

TABLE 4.—*List of forage organisms (arranged in order of frequency of occurrence) found in 39 yellowfin tuna stomachs with food, collected from area 2*

[Frequency of occurrence and volume are given for each taxon. See figure 1 for location of area of sampling]

Taxon	Frequency of occurrence		Volume	
	No.	Percent	Ml.	Percent
Fishes:				
Unidentifiable	33	84.6	602.3	20.3
Carangidae				
Decapterus spp.	4	10.2	92.7	3.1
Decapterus punctatus	3	7.6	38.0	1.3
Vomer setapinnis	3	7.6	2.1	0.1
Caranx spp.	1	2.5	1.0	<0.1
Caranx bartholomaei	1	2.5	8.2	0.3
Uraspis sp.	1	2.5		
Other Carangidae	11	28.2	90.5	3.0
Serranidae				
Paranthias furcifer	21	53.8	1689.5	56.9
Scombridae				
Auxis spp.	7	17.9	20.4	0.7
Scomber spp.	1	2.5	1.5	<0.1
Other Scombridae	12	30.7	71.7	2.4
Chaetodontidae				
Holacanthus spp.	8	20.5	6.2	0.2
Chaetodon spp.	2	5.1	0.9	<0.1
Dactylopteridae				
Dactylopterus volitans	9	23.0	96.2	3.2
Balistidae				
Balistes spp.	3	7.6	7.2	0.2
Xanthichthys ringens	2	5.1	3.7	<0.1
Aranthigaster spheroides	1	2.5	2.0	0.1
Other Balistidae	1	2.5	1.0	<0.1
Bramidae				
Collybus drachme	5	12.8	8.2	0.3
Collybus sp.	1	2.5	3.0	0.1
Other Bramidae	1	2.5	0.3	<0.1
Gempylidae				
Gempylus serpens	3	7.6	12.1	0.4
Other Gempylidae	3	7.6	2.1	0.1
Tetraodontidae				
Cantherines sp.	1	2.5	2.3	0.1
Cantherines pullus	3	7.6	9.6	0.3
Sphaeroides spp.	2	5.1	1.2	<0.1
Holocentridae				
Myripristis jacobus	1	2.5	2.0	<0.1
Holocentrus sp.	1	2.5	0.1	<0.1
Holocentrus ascensionis	1	2.5	1.5	<0.1
Holocentrus verillarius	1	2.5	0.2	<0.1
Other Holocentridae	1	2.5	1.0	<0.1

TABLE 4.—*List of forage organisms (arranged in order of frequency of occurrence) found in 39 yellowfin tuna stomachs with food, collected from area 2*—Continued

Taxon	Frequency of occurrence		Volume	
	No.	Percent	Ml.	Percent
Acanthuridae				
Acanthurus bahianus	1	2.5	0.7	<0.1
Acanthurus chirurgus	1	2.5	1.4	<0.1
Acanthurus spp.	1	2.5	0.8	<0.1
Other Acanthuridae	2	5.1	2.2	<0.1
Syngnathidae				
Syngnathus spp.	2	5.1	0.2	<0.1
Stromateidae				
Cubiceps spp.	1	2.5	5.1	0.2
Other Stromateidae	1	2.5	0.7	<0.1
Molidae				
Masturus lanceolatus	1	2.5	0.6	<0.1
Other Molidae	1	2.5	1.0	<0.1
Congridae	2	5.1	0.4	<0.1
Monacanthidae	1	2.5	1.0	<0.1
Ostraciidae				
Lactophrys spp.	1	2.5	0.2	<0.1
Priacanthidae				
Pseudopriacanthus altus	1	2.5	1.0	<0.1
Fistulariidae	1	2.5	0.2	<0.1
Anguilloidei	1	2.5	0.3	<0.1
Belonidae	1	2.5	0.5	<0.1
Coryphaenidae				
Coryphaena spp.	1	2.5	20.0	0.7
Pomacentridae				
Eupomacentrus sp.	1	2.5	0.1	<0.1
Chiasmodontidae				
Pseudoscopelus sp.	1	2.5		
Mollusks:				
Cephalopoda				
Teuthoidea				
Ommastrephidae	9	23.0	68.4	2.3
Illex illecebrosus	1	2.5	11.0	0.4
Enoploteuthidae	1	2.5	0.5	<0.1
Other Teuthoidea	5	12.8	29.2	1.0
Other Cephalopoda	5	12.8	22.8	0.8
Crustaceans:				
Decapoda				
Brachyura (megalopae)	7	17.9	2.1	0.1
Raninidae (megalopae)	7	17.9	1.7	0.1
Grapsidae (megalopae)	7	2.5	0.2	<0.1
Stomatopoda (larval forms)	7	17.9	8.5	0.3
Macrura-Natantia				
Penaeidae				
Ceratapsis sp.	1	2.5	0.4	<0.1
Ceratapsis petiti	2	5.1	2.5	0.1
Amphipoda (Hyperiidea)	3	7.6	0.7	<0.1
Mysidacea	1	2.5	1.5	<0.1
Miscellaneous:				
Unidentifiable invertebrates	5	12.8	2.9	0.1

TABLE 5.—*List of forage organisms (arranged in order of frequency of occurrence) found in 257 skipjack tuna stomachs with food, collected from area 3*

[Frequency of occurrence and volume are given for each taxon. See figure 1 for location of area of sampling]

Taxon	Frequency of occurrence		Volume	
	No.	Percent	Ml.	Percent
Fishes:				
Unidentifiable	91	35.4	367.2	20.3
Gempylidae				
Promethichthys sp.	1	0.4	0.6	<0.1
Promethichthys prometheus	5	1.9	33.4	1.8
Nesiarchus sp.	1	0.4	1.8	<0.1
Gempylus serpens	1	0.4	0.1	<0.1
Other Gempylidae	9	3.5	46.1	2.5
Carangidae				
Vomer setapinnis	11	4.3	8.4	0.5
Selene vomer	1	0.4	0.6	<0.1
Decapterus spp.	1	0.4	2.0	<0.1
Other Carangidae	3	1.2	17.2	1.0
Serranidae	9	3.5	28.8	1.6
Acanthuridae				
Acanthurus spp.	2	0.8	2.4	0.1
Acanthurus monroviae	6	2.3	6.4	0.4
Scombridae				
Auxis spp.	2	0.8	16.2	0.9
Euthynnus alletteratus	1	0.4	<0.1	<0.1
Other Scombridae	4	1.6	7.9	0.4
Tetraodontidae				
Sphaeroides spp.	3	1.2	4.9	0.3
Other Tetraodontidae	3	1.2	0.6	<0.1
Bothidae	5	1.9	4.2	0.2
Bramidae				
Collybus drachme	1	0.4	1.7	<0.1
Brama rayi	1	0.4	0.8	<0.1
Other Bramidae	3	1.2	2.9	0.2
Anguilloidei	3	1.2	0.6	<0.1
Chiasmodontidae				
Pseudoscopelus sp.	3	1.2	7.8	0.4
Syngnathidae				
Hippocampus spp.	1	0.4	0.1	<0.1
Other Syngnathidae	2	0.8	0.6	<0.1
Scorpaenidae				
Scorpaena spp.	2	0.8	1.1	<0.1
Other Scorpaenidae	1	0.4	0.5	<0.1
Dactylopteridae				
Dactylopterus volitans	3	1.2	2.0	0.1
Chaetodontidae				
Chaetodon spp.	2	0.8	1.7	<0.1
Priacanthidae	2	0.8	2.6	0.1
Paralepididae				
Paralepis spp.	1	0.4	68.0	3.8
Other Paralepididae	1	0.4	3.5	0.2
Monacanthidae				
Monacanthus spp.	1	0.4	0.8	<0.1
Balistidae	1	0.4	0.7	<0.1
Trichiuridae	1	0.4	1.5	<0.1
Synodontidae				
Synodus spp.	1	0.4	0.1	<0.1
Congridae	1	0.4	0.2	0.1
Myctophidae	1	0.4	0.2	0.1
Mollusks:				
Cephalopoda (adults and juveniles)				
Octopoda				
Argonauta sp.	1	0.4	0.5	<0.1
Other Octopoda	1	0.4	3.2	0.2
Teuthoidea				
Illex illecebrosus	8	3.1	47.7	2.6
Ommastrephidae	5	1.9	34.3	1.9
Ommastrephes pteropus	1	0.4	19.0	1.0
Other Teuthoidea	2	0.8	1.6	0.1
Gastropoda (adults)				
Heteropoda				
Oxygyrus keraudreni	13	5.1	2.0	0.1
Atlanta sp.	4	1.6	0.4	<0.1
Protatlanta sp.	1	0.4	0.1	<0.1
Atlantidae	1	0.4	0.1	<0.1
Pteropoda				
Diacria trispinosa	9	3.5	1.3	<0.1
Cavolinia spp.	5	1.9	0.5	<0.1
Cavolinia longirostris	3	1.2	0.3	<0.1
Cavolinia uncinata	5	1.9	17.5	0.1
Opisthobranchia	1	0.4	0.1	<0.1
Other Cephalopoda	40	15.6	89.9	5.0
Other mollusks	2	0.8	0.2	<0.1
Crustaceans:				
Stomatopoda (larval forms)	122	47.5	452.8	25.0
Decapoda				
Brachyura (megalopae)	110	42.8	343.6	19.0
Raninidae (megalopae)	8	3.1	1.4	0.1
Grapsidae (megalopae)	1	0.4	0.4	<0.1
Anomura				
Paguridea (all Glaucothoe)				
Dardanus spp.	3	1.2	0.4	<0.1
Dardanus arrosor	1	0.4	0.3	<0.1
Dardanus pectinatus	6	2.3	5.9	0.3
Petrochirus pustulatus	3	1.2	0.5	<0.1
Diogenidae	1	0.4	1.2	<0.1
Macrura-Natantia				
Penaeidae (all larvae)				
Ceratapsis spp.	1	0.4	0.1	<0.1
Ceratapsis monstrosa	1	0.4	1.0	<0.1
Other Macrura-Natantia	2	0.8	1.2	<0.1

TABLE 5.—*List of forage organisms (arranged in order of frequency of occurrence) found in 257 skipjack tuna stomachs with food, collected from area 3*—Continued

Taxon	Frequency of occurrence		Volume	
	No.	*Percent*	*Ml.*	*Percent*
Caridea (larvae and juveniles)	4	1.6	0.6	<0.1
Brachycarpus biunguiculatus	4	1.6	0.6	<0.1
Heterocarpus ensifer	1	0.4	2.9	0.2
Enoplometopus sp.	1	0.4	0.4	<0.1
Palaemonidae	1	0.4	0.1	<0.1
Stenopodidae	1	0.4	0.6	<0.1
Macrura-Reptantia (all Phyllosoma larvae)				
Scyllarus sp.	5	1.9	2.0	0.1
Panulirus rissoni	1	0.4	0.1	<0.1
Other Macrura-Raptantia	2	1.9	1.2	<0.1
Amphipoda (Hyperiidea) (adults and juveniles)				
Brachyscelus spp.	27	10.5	16.5	0.9
Phrosina semilunata	20	7.8	7.4	0.4
Phronima sedentaria	6	2.3	1.3	0.1
Oxycephalus clausii	5	1.9	2.5	0.1
Platyscelus ovoides	5	1.9	2.3	0.1
Streetsia challengeri	3	1.2	1.0	<0.1
Streetsia porcela	2	0.8	0.2	<0.1
Anchylomera blossevillei	2	0.8	0.3	<0.1
Parapronoe crustulum	1	0.4	0.7	<0.1
Other Hyperiidea	57	22.2	19.4	1.1
Euphausicea (adults)	2	0.8	0.2	<0.1
Mysidacea	3	1.2	0.5	<0.1
Miscellaneous:				
Unidentifiable invertebrates	59	22.9	59.0	3.3

TABLE 6.—*List of forage organisms (arranged in order of frequency of occurrence) found in 520 yellowfin tuna stomachs with food, collected from area 3*

[Frequency of occurrence and volume are given for each taxon. See figure 1 for location of area of sampling]

Taxon	Frequency of occurrence		Volume	
	No.	*Percent*	*Ml.*	*Percent*
Fishes:				
Unidentifiable	268	51.5	845.4	13.4
Carangidae				
Vomer sp.	3	0.6	1.4	<0.1
Vomer setapinnis	32	6.1	29.0	0.5
Decapterus spp.	5	0.9	33.9	0.5
Selar crumenopthalmus	4	0.8	2,144.0	34.1
Uraspis sp.	1	0.2	3.5	<0.1
Other Carangidae	11	2.1	36.5	0.6
Tetraodontidae				
Sphaeroides spp.	10	1.9	17.0	0.3
Canthigaster sp.	1	0.1	42.0	0.7
Canthigaster rostratus	3	0.6	27.6	0.4
Lagocephalus lagocephalus	1	0.2	2.0	<0.1
Sphaeroides spengleri	1	0.2	1.6	<0.1
Other Tetraodontidae	24	4.6	115.2	1.8
Gempylidae				
Promethichthys prometheus	4	0.8	21.0	0.3
Nesiarchus nasutus	3	0.6	3.7	<0.1
Other Gempylidae	32	6.1	81.0	1.3
Serranidae				
Anthias anthias	2	0.4	2.0	<0.1
Paranthias furcifer	2	0.4	0.3	<0.1
Other Serranidae	18	3.5	11.0	0.2
Priacanthidae				
Priacanthus spp.	4	0.8	2.5	<0.1
Priacanthus cruentatus	2	0.4	2.5	<0.1
Priacanthus arenatus	1	0.2	1.2	<0.1
Cookeolus boops	1	0.2	1.1	<0.1
Other Priacanthidae	10	1.9	9.3	0.1
Scombridae				
Auxis spp.	5	0.9	19.2	0.3
Scomber japonicus	2	0.4	18.0	0.3
Other Scombridae	9	1.7	7.7	0.1
Bramidae				
Collybus drachme	8	1.5	5.0	0.1
Pterycombus sp.	1	0.2	1.7	<0.1
Other Bramidae	1	0.2	0.3	<0.1

TABLE 6.—*List of forage organisms (arranged in order of frequency of occurrence) found in 520 yellowfin tuna stomachs with food, collected from area 3*—Continued

Taxon	Frequency of occurrence		Volume	
	No.	*Percent*	*Ml.*	*Percent*
Zeidae				
Zenion hololepis	9	1.7	270.5	4.3
Dactylopteridae				
Dactylopterus volitans	8	1.5	10.2	0.2
Chaetodontidae				
Chaetodon spp.	3	0.6	1.1	<0.1
Chaetodon marcelae	5	0.9	7.4	0.1
Bothidae	5	0.9	2.7	<0.1
Gonostomatidae				
Maurolicus sp.	1	0.2	0.5	<0.1
Maurolicus mulleri	3	0.6	33.0	0.5
Other Gonostomatidae	1	0.2	0.7	<0.1
Exocoetidae				
Hirundichthys sp.	1	0.2	47.0	0.7
Other Exocoetidae	4	0.8	221.3	3.5
Scorpaenidae				
Scorpaena spp.	1	0.2	2.1	<0.1
Other Scorpaenidae	4	0.8	6.2	0.1
Ostraciontidae	4	0.8	2.5	<0.1
Stromateidae	3	0.6	6.0	0.1
Monacanthidae	3	0.6	12.0	0.2
Congridae				
Ariosoma sp.	2	0.4	9.9	0.2
Other Congridae	1	0.2	0.5	<0.1
Nomeidae				
Cubiceps spp.	2	0.4	3.3	<0.1
Cubiceps gracillis	1	0.2	2.5	<0.1
Chiasmodontidae				
Pseudoscopelus sp.	2	0.4	3.2	<0.1
Aulostomidae				
Aulostomus maculatus	2	0.4	8.9	0.1
Anguilloidei	2	0.4	17.3	0.3
Paralepididae				
Paralepis spp.	2	0.4	167.0	2.6
Trichiuridae	2	0.4	30.5	0.5
Acanthuridae				
Acanthurus monroviae	1	0.2	0.4	<0.1
Other Acanthuridae	1	0.2	0.8	<0.1
Syngnathidae				
Hippocampus spp.	1	0.2	1.6	<0.1
Dorichthus spp.	1	0.2	0.6	<0.1
Grammicolepididae				
Xenolepidichthys sp.	1	0.2	3.0	<0.1
Ostraciidae				
Ostracion sp.	1	0.2	1.1	<0.1
Scorpaenoidei	1	0.2	2.0	<0.1
Synodontidae				
Synodus spp.	1	0.2	1.0	<0.1
Uranoscopidae	1	0.2	0.2	<0.1
Triglidae				
Lepidotrigla spp.	1	0.2	0.2	<0.1
Pomacentridae	1	0.2	0.2	<0.1
Scombroidei	1	0.2	0.4	<0.1
Stomiatoidei	1	0.2	0.2	<0.1
Eugraulidae	1	0.2	0.3	<0.1
Caproidae				
Antigonia capros	1	0.2	1.2	<0.1
Anoplogasteridae	1	0.2	2.5	<0.1
Callionymidae	1	0.2	0.1	<0.1
Holocentridae				
Holocentrus spp.	1	0.2	0.3	<0.1
Berycoidei	1	0.2	0.4	<0.1
Blenniidae				
Blennius spp.	1	0.2	0.4	<0.1
Balistidae	1	0.2	0.9	<0.1
Mollusks (juveniles and adults):				
Cephalopoda (adults and juveniles)				
Octopoda				
Argonauta sp.	2	0.4	1.3	0.1
Other Octopoda	15	2.9	27.5	0.4
Teuthoidea				
Ommastrephidae	21	4.0	117.0	1.9
Ommastrephes spp.	2	0.4	0.5	0.1
Ommastrephes pteropus	4	0.8	17.0	0.3
Illex illecebrosus	17	3.3	174.3	2.8
Abralia sp.	2	0.4	1.0	0.1
Sepioidea	1	0.2	2.3	<0.1
Other Teuthoidea	19	3.6	76.6	1.2
Other cephalopods	173	33.3	332.9	5.3
Gastropoda				
Heteropoda				
Oxygyrus keraudreni	6	1.1	0.7	<0.1

TABLE 6.—*List of forage organisms (arranged in order of frequency of occurrence) found in 520 yellowfin tuna stomachs with food, collected from area 3*—Continued

Taxon	Frequency of occurrence		Volume	
	No.	Percent	Ml.	Percent
Pteropoda				
Cavolinia sp.	1	0.2	0.1	0.1
Cavolinia uncinata	1	0.2	0.1	0.1
Atlantidae	1	0.2	0.1	0.1
Tonnidae				
Tonna galea (larvae)	5	0.9	0.7	<0.1
Opisthobranchia	1	0.1	0.1	0.1
Other mollusks	3	0.6	0.3	<0.1
Crustaceans:				
Stomatopoda (larval forms)				
Lysiosquilla sp.	1	0.2	2.0	<0.1
Other Stomatopoda	366	70.4	573.4	9.1
Decapoda				
Brachyura (megalopae)	107	20.6	104.1	1.6
Raninidae (megalopae)	29	5.6	3.0	<0.1
Lyreidus sp. (megalopae)	1	0.2	0.1	<0.1
Grapsidae (megalopae)	4	0.8	2.0	<0.1
Anomura				
Paguridea (all Glaucothoe)				
Dardanus spp.	16	3.1	5.6	0.1
Dardanus pectinatus	12	2.3	2.2	<0.1
Dardanus arrosor	2	0.4	0.3	<0.1
Petrochirus pustulatus	4	0.8	0.5	<0.1
Diogenidae	1	0.2	0.1	<0.1
Other Anomura	31	5.9	13.8	0.2
Macrura-Natantia (Caridea—adults, juveniles, and larvae)				
Heterocarpus ensifer	26	5.0	255.6	4.1
Brachycarpus biunguiculatus	17	3.2	4.4	0.1
Stenopus hispidus	1	0.2	0.2	<0.1

TABLE 6.—*List of forage organisms (arranged in order of frequency of occurrence) found in 520 yellowfin tuna stomachs with food, collected from area 3*—Continued

Taxon	Frequency of occurrence		Volume	
	No.	Percent	Ml.	Percent
Enoplometopus sp.	1	0.2	0.4	<0.1
Lucifer sp.	1	0.2	0.1	<0.1
Other Macrura-Natantia	20	3.8	7.6	0.1
Macrura-Reptantia (all Phyllosomae)				
Scyllarus sp.	26	5.0	5.3	0.1
Scylarides sp.	3	0.6	1.6	<0.1
Panulirus rissoni	1	0.2	0.2	<0.1
Other Macrura-Reptantia	4	0.8	8.0	<0.1
Amphipoda (Hyperiidea)				
Brachyscelus spp.	67	12.9	12.3	0.2
Phrosina semilunata	55	10.6	17.3	0.2
Phronima sedentaria	19	3.6	2.7	<0.1
Streetsia challengeri	5	0.9	0.5	<0.1
Platyscelus ovoides	5	0.9	0.9	<0.1
Platyscelus serratulus	3	0.6	0.2	<0.1
Oxycephalus clausii	4	0.8	0.5	<0.1
Vibilia cultripes	4	0.8	0.7	<0.1
Anchylomera blossevillei	3	0.6	0.3	<0.1
Sympronoe parva	2	0.4	0.2	<0.1
Vibilia sp.	2	0.4	0.2	<0.1
Phronima spp.	1	0.2	0.1	<0.1
Pararpronoe crustulum	1	0.2	0.2	<0.1
Other Hyperiidea	45	8.6	10.4	0.2
Euphausiacea	3	0.6	0.6	<0.1
Mysidaecea	1	0.2	0.1	<0.1
Copepoda				
Euchacta sp.	1	0.2	0.1	<0.1
Miscellaneous:				
Unidentifiable invertebrates	129	24.8	134.1	2.1

AN ESTIMATE OF MORTALITY OF CHINOOK SALMON IN THE COLUMBIA RIVER NEAR BONNEVILLE DAM DURING THE SUMMER RUN OF 1955

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ABSTRACT

In 1955 the Oregon Fish Commission estimated the numbers of dead chinook salmon, *Oncorhynchus tshawytscha*, near Bonneville Dam and studied the probable causes of death.

The estimates of numbers of dead fish were made from ratios of tagged to untagged floating carcasses below the dam. Tagged salmon carcasses were released at the dam, and the river below the dam was searched systematically to recover tagged and untagged carcasses. The introduced tagged carcasses and the untagged carcasses of fish that died in the river were assumed to have equal chances of recovery, provided they were not too severely mutilated to be recoverable. This assumption was verified experimentally.

On June 30 and July 1, 1955, when riverflows were relatively high, 1,169 tagged chinook salmon carcasses were released at Bonneville Dam. Thirty-one tagged and 117 untagged carcasses were recovered in searches downstream from the release point. On the basis of these recoveries, an estimated 4,412 summer-run chinook salmon died near the dam between June 21 and July 10. On the basis of this estimate, 16.8 percent of the total chinook salmon run died at Bonneville Dam in this period.

The numbers of floating carcasses in 1954 and 1955 were directly related to spillway discharge; greatest numbers of floating dead fish coincided with Columbia River flows in excess of 7,100 c.m.s. At Bonneville Dam fall chinook salmon runs have never been subjected to flows above 7,100 c.m.s. (killing flows); spring runs are exposed to such flows in some years; and summer runs nearly always encounter such flows. Water temperature, turbidity, disease, and injuries from gill nets did not affect the number of carcasses. Although the specific causes of death and the precise areas at Bonneville Dam where death occurred were not determined in our study, the major source of chinook salmon mortality was associated with the spillway during high flows. Other investigators subsequently demonstrated that during high flows the Columbia River that has plunged over dam spillways is supersaturated with atmospheric nitrogen. This supersaturation may be one of the principal causes of death of fish at mainstem dams.

Bonneville Dam is only about 18.3 m. high, and hundreds of thousands of salmon successfully negotiate the fishways each year; yet many salmon are killed during periods of high flow. Complacency about the efficiency of salmon passage over large dams is, therefore, unwarranted, even when elaborate well-designed passage facilities are present and few dead or injured fish are noticed.

The problem of facilitating passage of anadromous fish over dams and evaluating the effects of dams on the fish has become a matter of increasing importance and concern because of the steady increase in the number of dams in the past 2 decades. Each dam is an impediment to migratory fish.

The Columbia River, one of the greatest rivers in the world for chinook salmon, *Oncorhynchus tshawytscha*, now has 11 dams across the main stem and numerous dams across tributaries. Bonneville Dam, the first dam on the lower Columbia River, was completed in 1938; it is 227 km. from the river mouth. Before its construction, anadromous fish migrated with little difficulty into the upper Columbia and Snake Rivers and their tributaries to spawn. The lower river had two natural barriers—Cascade Rapids and Celilo

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Falls—but fish could readily pass these except in periods of extremely low riverflow. Cascade Rapids was inundated by Bonneville Dam in 1938; Celilo Falls by The Dalles Dam in 1957.

Each year Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, that spawn above Bonneville Dam yield several million dollars to commercial and sport fisheries in the river and ocean. Because of the great value of these fish, it is important to ensure that they pass over the dam with a minimum of loss and delay.

Hanson, Zimmer, and Donaldson (1950) counted many dead fish in the river below Bonneville Dam in various seasons and years, and fishermen in boats below the dam often observed floating dead fish or dying fish on the surface. Chinook salmon were reported most frequently, but other species were also noted: sockeye or Columbia River blueback salmon, *O. nerka*; steelhead trout; American shad, *Alosa sapidissima*; white sturgeon, *Acipenser transmontanus*; carp, *Cyprinus carpio*; and Pacific lamprey, *Entosphenus tridentatus*. Biologists and fishermen suspected that many of these fish died from attempting to find a route over the dam or from being swept downstream through the spillway after ascending a series of gravity-flow fish ladders, the principal means for fish to migrate over the dam. Although many of the fish seemed to negotiate the ladders satisfactorily, Schoning and Johnson (1956) estimated that chinook salmon were delayed an average of 2.6 to 3.0 days in their migration.

This paper reports a study of the magnitude and possible causes of the mortality of fish at Bonneville Dam, with particular reference to the summer run of chinook salmon, which is believed to be more adversely affected than other runs.

Bonneville Dam (fig. 1) consists of two concrete sections—the spillway and the powerhouse—

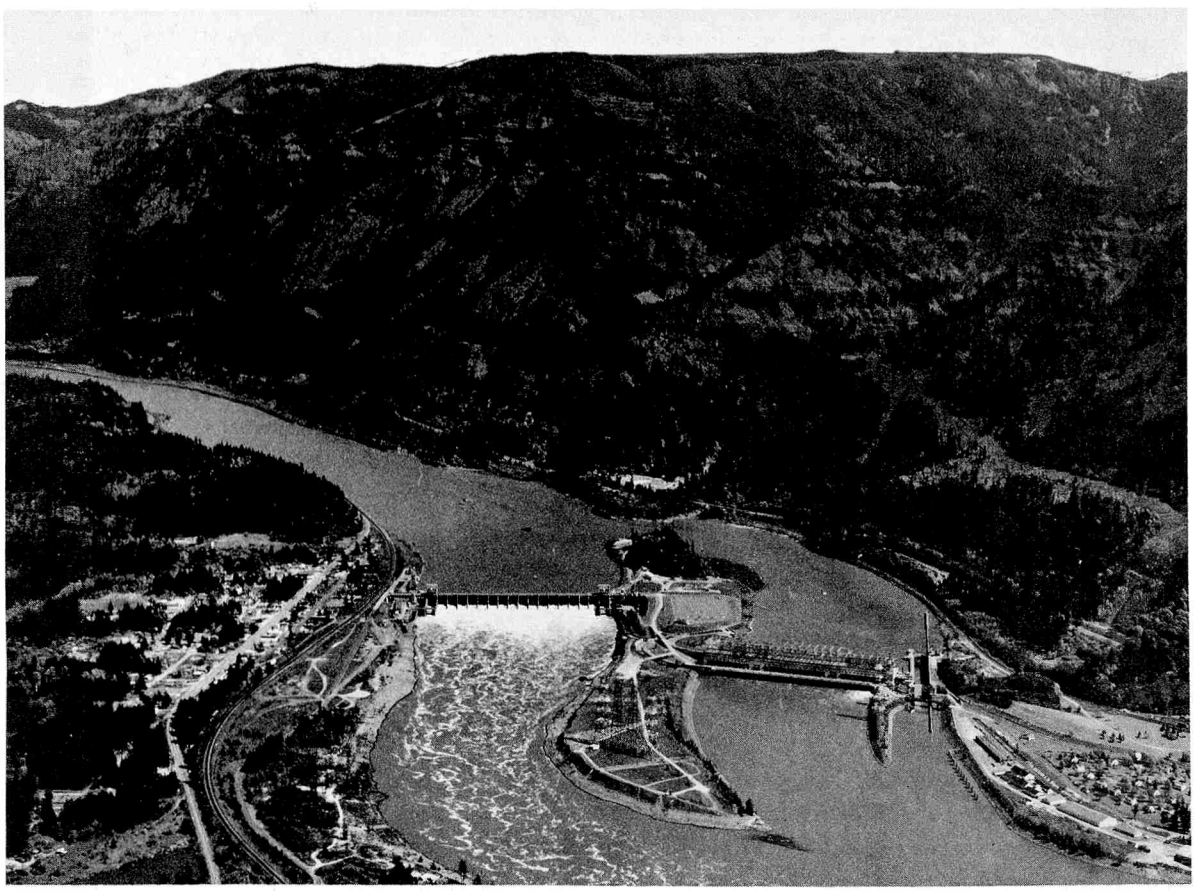

FIGURE 1.—Bonneville Dam, showing the spillway and powerhouse sections and the difference in turbulence between the two sections. Photo taken April 29, 1958, when spillway flow was 4,000 c.m.s. and powerhouse flow, 2,700 c.m.s. (Photo courtesy of U.S. Army Corps of Engineers.)

which are separated by Bradford Island. The spillway spans the Columbia River north of the island, and the powerhouse spans the south channel. The spillway has eighteen 15.2-m.-wide gates that release water not needed for power generation. To attract fish to the adjacent ladder entrances, the gate at each end of the spillway discharges water (except during very high or very low flows). The gates are the vertical-lift type, and water is released under them at a maximum forebay depth of about 17.8 m. (fig. 2). The spillway extends downstream from the gates to form two rows of concrete baffles that partially dissipate the energy of the water rushing under the gates. The flow through the spillway varies from a few cubic meters per second to several thousand.

Bonneville Dam has little water storage capacity. Differences in the water level between the forebay and the tail water range from 12.1 to 18.3 m., depending on riverflow and power generation requirements. The powerhouse contains 10 Kaplan turbines, each with a maximum discharge capacity of 410 c.m.s. Flow through the powerhouse is nearly constant throughout the year, but flow through the spillway varies greatly.

Facilities for passage of adult salmon upstream over the dam are extensive and complex. Most fish go up two gravity-flow ladders, which have slopes of 0.3 m. in 6 m. The Washington shore (north) ladder has a single entrance adjacent to the north end of the spillway and exits into the forebay about 120 m. upstream from the dam. The Bradford Island (south) ladder has three entrances and a single exit into the forebay about 120 m. above the powerhouse on the south side of Bradford Island. One entrance of the Bradford Island ladder is adjacent to the south end of the spillway; another is at the north end of the powerhouse; and the third, consisting of many small entrances, is across the powerhouse above the draft tubes.

Information on dead fish below Bonneville Dam comes from several sources. The principal sources are Federal and State agencies: the BCF (Bureau of Commercial Fisheries), U.S. Army Corps of Engineers, Oregon Fish Commission, and Washington Department of Fisheries. Some information is also provided by commercial fishermen, who spend much time on the river during the major fish migrations; salmon sport fishermen; and

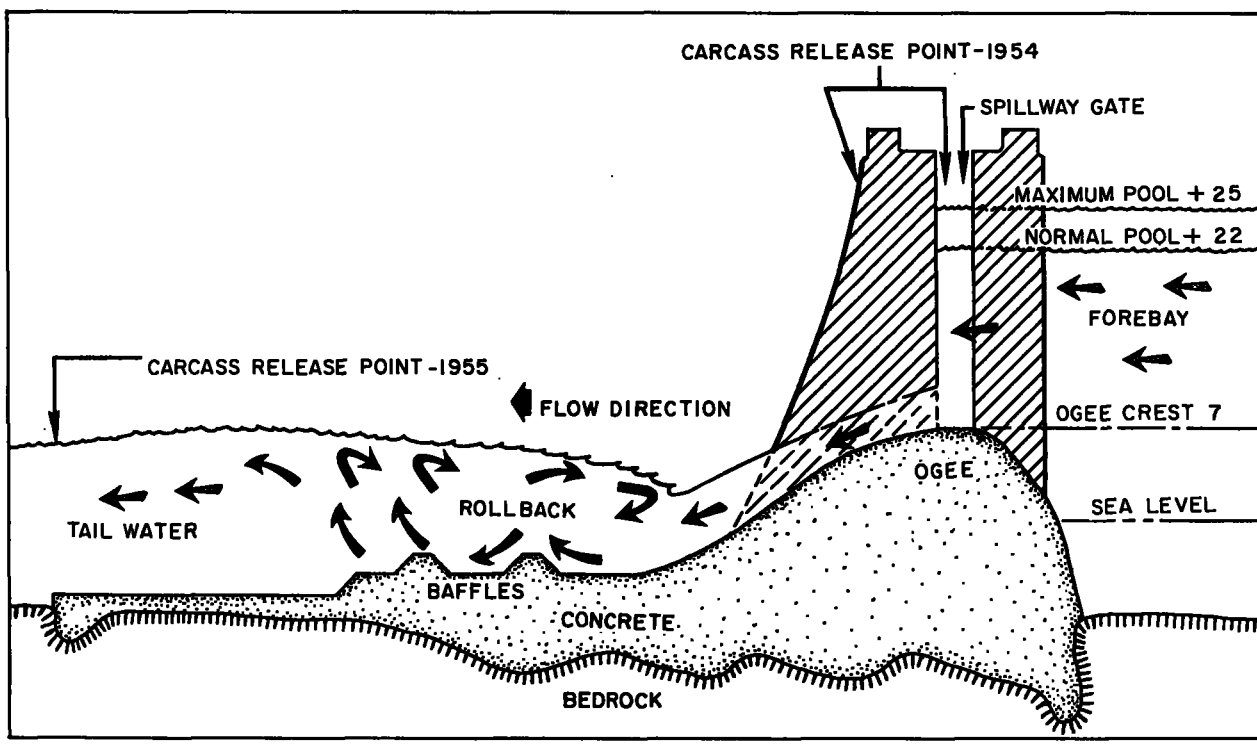

FIGURE 2.—Bonneville Dam spillway construction and flow cross-sectional diagram (from U.S. Army Corps of Engineers drawing). Elevations are in meters above mean sea level.

sturgeon sport fishermen, who seek salmon carcasses for bait.

Until our study, only one extensive effort had been made to evaluate the significance of dead fish near the dam. In 1946 FWS (U.S. Fish and Wildlife Service) and the U.S. Army Corps of Engineers investigated the causes of injuries and deaths of fish (Hanson et al., 1950). The major emphasis of that study was on counting, from boats, the floating dead fish near the dam during the main part of the chinook salmon fall migration. The study did not provide the information needed to determine the relation between numbers of floating dead salmon, numbers of dead salmon not observed, and numbers of salmon surviving to continue their upstream spawning migration.

Sporadic observations in other years by biologists and fishermen also failed to provide information that could be used to evaluate the significance of floating dead salmon. To illustrate the difficulty of interpreting such information, we cite two examples of observations made at a time when unusually large numbers of floating dead salmon were in the Columbia River.

The first observation was on September 9, 1943. Arnie J. Suomela, Fishery Biologist with the Washington State Department of Fisheries, spent 8 hours searching from a boat for dead salmon between Bonneville Dam and Multnomah Falls. He found 146 floating chinook salmon, nine steelhead trout, and one sockeye salmon; the following statement is from his report. "Checked Oregon shore and river on trip down to Multnomah Falls. Only two salmon were found on this part of trip. The first floating dead fish were found at Butler's Eddy, at 3:05 p.m.; and floaters were found from that point to below the spillway at the dam. This observation definitely traces the mortality to the north spillway channel and it is reasonable to believe that the mortality is occurring at the spillway."[4]

The second observation was in the spring of 1952. The Oregonian newspaper for June 12, 1952, reported: "A commercial fisherman . . . recently . . . found 'thousands' of dead chinook salmon between Martins Slough [102 km. downstream from Bonneville Dam] and the mouth of the Lewis River. [He] said the beaches were littered with spring chinook. 'You could find more as you get closer to the Dam.' "

[4]Unpublished field notes, Washington State Department of Fisheries.

The inadequacy of the simple observational method in assessing the true magnitude of mortality is exemplified further in a classic study by the International Pacific Salmon Fisheries Commission. At Hell's Gate on the Fraser River, salmon were blocked by turbulent water at certain riverflows, and an annual loss of thousands (even millions) of salmon there has been well documented (Thompson, 1945; Talbot, 1950; Jackson, 1950). Although a great mortality was suspected, only a relatively small number of moribund or dead fish were sighted on extensive searches downstream from Hell's Gate over a period of many years. Thompson (1945: 96) described the situation at Hell's Gate in 1941: "It could be said that numbers of them [sockeye salmon] were observed approaching death, having reached a condition which obviously precluded their passage through any difficult currents; yet simple observation could not prove that death actually occurred nor that the percentage dying was very high. To find even hundreds of fish near death along the riffles in the river, or in the creeks did not necessarily prove that a great part of the run perished below. Some form of evidence more conclusive was necessary."

Thus, on neither the Columbia nor Fraser Rivers did simple observations of dead fish provide a basis for estimating the true mortality. For this reason, we devised a different method.

Our aims were (1) to estimate the mortality of adult chinook salmon near Bonneville Dam during a period when large numbers of salmon were passing the dam and (2) to evaluate factors contributing to or associated with these deaths, such as streamflow, temperature, turbidity, commercial fishing, fish passage facilities, and disease. Throughout this paper, data on counts of fish at Bonneville Dam and on flow, turbidity, and temperature of the Columbia River are from U.S. Army Corps of Engineers (1943–56).

We first examined records of observations of dead fish and counts of chinook salmon through the ladders at the dam to determine when maximum mortality had occurred. Biologists, commercial fishermen, and boat moorage operators near the dam generally reported that the number of floating dead salmon was greatest in the spring, coincident with high riverflows and large numbers of chinook salmon in the river. We, therefore, selected the spring period of high riverflows for

intensive investigation. (We subsequently found that summer is usually the period of maximum mortality.)

The method we used to estimate the total numbers of dead fish was based on a mark-and-recovery technique. Preparatory to making the estimates, we determined the relative floating qualities of tagged experimental (killed, frozen, and thawed) and "natural" river-killed salmon, located points where salmon lodge downstream from the dam before they float, and made systematic surveys from boats and airplanes to determine the best sites for observing dead fish near the dam. Searchers in boats below Bonneville Dam recovered all the tagged and untagged floating salmon used for the population estimate.

BCF contracted with the Oregon Fish Commission to make this study.

ABUNDANCE AND LOCATION OF FLOATING SALMON CARCASSES

Dead salmon in the Columbia River are most evident as "floaters" (partially decomposed floating carcasses); hereafter in this paper this term refers to any floating dead salmonid. Floaters are carried downstream by the current and can usually be seen from a considerable distance. We searched systematically from boats and aircraft in 1954 and 1955 and also tagged and recovered floaters to learn how they disperse in the Columbia River. We also introduced tagged dead chinook salmon into the river at Bonneville Dam in both years to provide a basis for estimating total numbers of dead fish; in 1955 the observations from boats were used to estimate the mortality of summer chinook salmon.

SEARCHES FROM BOATS

1954

In 1954 we searched for floaters downstream from Bonneville Dam during three periods (table 1). Five boats were used; four were 4.9 to 5.5-m. skiffs propelled by outboard motors, and the fifth was a 7.9-m. inboard Columbia River gill-netter. The skiffs were usually manned by one person and the large boat by two. Efficiency of observations was assumed to be equal for all boats. Each observer was equipped with Petersen disk tags, Polaroid[5] glasses, and a dip net to recover floating carcasses. Search time was recorded in hours and minutes. Table 1 shows the numbers of floaters (by species).

TABLE 1.—*Floaters observed during three search periods on Columbia River downstream from Bonneville Dam, July 12 to September 12, 1954, and numbers of chinook salmon floaters observed per hour of search*

Period of search	Floaters observed				Chinook floaters observed per hour of search
	Chinook salmon	Steelhead trout	Sockeye salmon	Unidentified salmonids	
	Number	*Number*	*Number*	*Number*	*Number*
July 12 to Aug. 5	30	7	8	1	1.1
Aug. 9–20	6	14	1	1	0.2
Sept. 4–12	99	54	2	4	0.8

The searches were all made relatively close to the dam. During the first search period (July 12 to August 5), observers in the five boats searched midstream and shoreline sections from the dam to the mouth of the Willamette River. In the early part of this period an additional observer was stationed on shore on a high dock at Ellsworth, Wash., where he could scan the main river channel with binoculars. The second search period (August 9–20) included the same areas. During the final search period (September 4–12), effort was reduced to a roving search from two boats between Ellsworth and the dam and observations from the Ellsworth dock. One of the two boats patrolled the 31 km. of river from Ellsworth to Cape Horn, and the other the 23 km. of river from Cape Horn to the dam (fig. 3).

1955

Searches by boat for floaters in 1955 were limited mainly to the main current in midstream on transects across the river channel at eight locations. The boats and equipment used by observers were the same as those used in 1954, and search time was again recorded in hours and minutes. The eight stations and their locations (fig. 3) were (1) St. Helens—93 km. below the dam, and 1.6 km. upstream from St. Helens, Oreg.; (2) Willamette—70 km. below the dam, immediately upstream from the confluence of the Willamette and Columbia Rivers; (3) Ellsworth—53 km. below the dam at Ellsworth, Wash.; (4) Reed Island—35 km. below the dam, immediately downstream from Reed Island; (5) Cape Horn—23 km. below the dam; (6) McGowan

[5] Trade name referred to in this publication does not imply endorsement of commercial product.

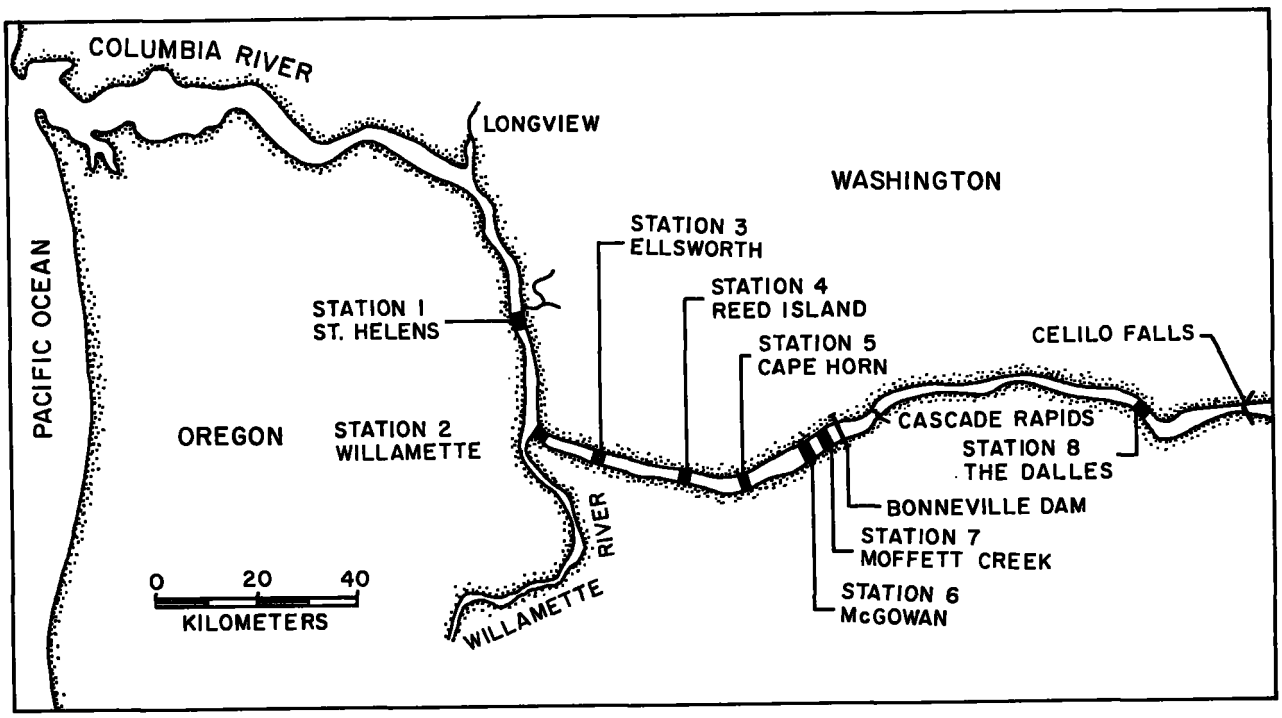

FIGURE 3.—Locations of search stations on Columbia River near Bonneville Dam where floaters were observed in 1954 and 1955.

—7 km. below the dam; (7) Moffett Creek—3 km. below the dam opposite the mouth of Moffett Creek; and (8) The Dalles—72 km. above the dam, 0.8 km. downstream from The Dalles, Oreg.

At each station, an observer in a boat roved back and forth across the river 8 hours a day on a transect perpendicular to the riverflow. All observations were recorded in one of three categories: river site—midstream search at a station; river vicinity—midstream search at other than an established station (usually en route to and from a station at the beginning and end of the day); and shore—search on foot alongshore (table 2). Eighty-two percent of the total search time was at river sites, 15 percent at river vicinities, and 3 percent on shore. Stations 6 and 7 were alternately manned by the same boat crew at different times, depending on visibility. Observations began on April 4 at stations 2, 4, 6, and 7 and on May 3 at station 8. The observer at station 1 was moved to station 5 at the end of June, and on July 12 the observer at station 4 was moved to station 3. A total of 1,666 hours and 50 minutes were spent on all searches in 1955 (table 2).

By the time the observations began in April, appreciable numbers of spring chinook salmon had passed Bonneville Dam. The numbers passing through the ladders increased rapidly in late April and reached a peak on May 2, when 13,763 fish were recorded. Only four chinook salmon floaters, or 0.02 per hour of search, were found in April at search stations, and only eight—again 0.02 per hour—were found in May (table 3). Thus, in April and May, when a record run of 170,205 spring chinook salmon passed the dam, the observers found only a few chinook salmon floaters at the four stations between St. Helens and the dam.

During the first half of June, only 11,551 chinook salmon passed the dam, but 13 chinook salmon floaters (0.07 per hour) were found downstream from the dam. In the second half of June, most of the summer chinook salmon run (33, 951) passed the dam, and searchers found an increasing number as floaters below the dam—0.23 per hour of search (table 3).

TABLE 2.—*Time observers spent searching in boats for floating salmon carcasses at eight stations on the Columbia River near Bonneville Dam, April 4 to July 22, 1955*

[See text for definition of search areas]

Station and month (station number in parentheses)	River site		River vicinity		Shore		Total	
	Hr.	*Min.*	*Hr.*	*Min.*	*Hr.*	*Min.*	*Hr.*	*Min.*
The Dalles (8)								
May	72	10	1	40	-------	35	74	25
June	55	15	----------		1	45	57	0
July	88	15	----------		----------		88	15
Total	215	40	1	40	2	20	219	40
Moffett Creek (7)								
April	12	35	----------		----------		12	35
June	11	10	----------		----------		11	10
Total	23	45	----------		----------		23	45
McGowan (6)								
April	17	40	12	25	----------		30	5
May	53	50	25	5	1	10	80	5
June	44	20	26	50	1	50	73	0
July	59	30	23	50	24	15	107	35
Total	175	20	88	10	27	15	290	45
Cape Horn (5)								
June	1	40	1	0	----------		2	40
July	79	50	28	50	1	20	110	0
Total	81	30	29	50	1	20	112	40
Reed Island (4)								
April	68	15	13	5	----------		81	20
May	78	5	12	10	-------	25	90	40
June	96	40	28	15	7	5	132	0
July	47	25	33	15	8	25	89	5
Total	290	25	86	45	15	55	393	5
Ellsworth (3)								
July	56	45	15	15	4	40	76	40
Total	56	45	15	15	4	40	76	40
Willamette (2)								
April	85	30	----------		----------		85	30
May	101	45	----------		----------		101	45
June	94	55	1	30	-------	45	97	10
July	92	35	2	35	7	30	102	40
Total	374	45	4	5	8	15	387	5
St. Helens (1)								
May	75	40	9	0	----------		84	40
June	67	40	10	50	----------		78	30
Total	143	20	19	50	----------		163	10
Grand total	1,361	30	245	35	59	45	1,666	50

The greatest numbers of floaters were found below the dam in July: between the dam and station 2, 182 chinook and 53 sockeye salmon floaters were recovered (0.40 chinook and 0.12 sockeye salmon per hour of search). Between July 1 and 15, 23,034 chinook and 199,095 sockeye salmon were counted over the dam. Thus, although counts of chinook salmon were declining, the rate of recovery of floaters in early July was much greater than in earlier periods—nearly double the next highest rate in June. Counts of salmon at the dam and floaters in the river were both declining by July 22 when the study ended.

Searches above the dam were limited to station 8 from May 3 to July 22. Chinook salmon floaters found per hour of search were: May, 0.0; June, 0.04; and July, 0.17.

Our experience in 1954 and 1955 demonstrated that floaters could be effectively counted by observers in boats.

TABLE 3.—*Chinook and sockeye salmon counted over Bonneville Dam, April 1 to July 15, 1955, and number found as floaters per search hour at stations below dam, April 4 to July 22, 1955*

Time period	Salmon counted		Floaters found [1]		Floaters per hour	
	Chinook salmon	Sockeye salmon	Chinook salmon	Sockeye salmon	Chinook salmon	Sockeye salmon
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
April 1–30	84,436	0	4	0	0.02	----------
May 1–31	85,769	77	8	0	.02	----------
June 1–15	11,551	68	13	0	.07	----------
June 16–30	33,951	21,855	45	0	.23	----------
July 1–15	23,034	199,095	182	53	.40	0.12

[1] Floaters found and search time spent on shore search area (table 2) not included.

SEARCHES FROM AIRCRAFT IN 1954 AND 1955

Synoptic observations of floaters in the Columbia River were needed to determine if at any given time the numbers of floaters were greater below dams on the river than above. The aerial survey method was chosen because Merrell had seen carcasses of chinook salmon on low-altitude spawning survey flights on the Columbia River and the upper Snake River in Idaho—a distance too great to cover with boat searches. At the time of our study the Columbia River had only two dams, Bonneville and McNary (237 km. up the Columbia River from Bonneville Dam).

A chartered two-place single-engine, high-wing monoplane with a cruising speed of about 120 km. per hour was used for all flights. The pilot sat in the rear seat, and a biologist in the front seat, from which point the visibility was excellent. A blind spot directly below the aircraft when it was in level flight did not significantly hamper observations. Merrell and Collins made all observations. Altitude varied between 15 and 100 m. The river was searched on both the upstream and downstream flights. Over sections where the river was wide, observations were confined to one side of the river on the first trip and to the opposite side on the return trip; less than half the total river surface could be observed in these sections. In narrower sections, particularly between The Dalles and McNary Dams, a greater portion of the river surface, and at times the entire width of

the river, could be seen clearly. Because all flights were made in the same manner, it is not important whether we saw all floaters; the significant point is that we determined the relative abundance of floaters.

Floaters could be seen easily at the low altitude at which observations were made. Although chinook salmon could usually be distinguished from other species by their relatively large size, all floaters were combined in interpreting the observations. Adverse light conditions and waves occasionally reduced the efficiency of the observations. To compensate for the glare on the water surface, the plane was flown on the side of the river toward the sun and the observers wore Polaroid glasses. Waves and whitecaps were the most serious problems because they reduced the distance at which carcasses could be seen. Fortunately, visibility was generally good on all flights. We recorded all floaters except in the rare instance when on the return trip we definitely recognized a carcass that we had counted before. We may have counted some twice but believe this seldom occurred.

We assumed that we saw a nearly constant proportion of the floaters present on each flight. Granting this assumption, the variations in numbers and distribution of floaters on different flights reflect real differences. In 1954, between July 16 and September 17, floaters were counted on 10 flights over the Columbia River between Longview, Wash., and the McNary Dam (320 km.). Figure 4 shows the numbers of floaters in 8-km. sections of the river on each flight. In 1955, between May 6 and September 13, floaters were counted on seven flights from the mouth of the Columbia River at Astoria, Oreg., to its confluence with the Snake River and up the Snake River to Lewiston, Idaho—a total distance of 720 km. Figure 5 shows the numbers of floaters in 8-km. sections of the area surveyed. The survey between Astoria, Oreg., and Lewiston, Idaho, extended over 2 days, July 14 and 15.

Floaters in both years were not uniformly distributed throughout the river but were consistently concentrated at certain locations. The greatest density was downstream from Bonneville Dam when riverflows were high or when relatively large numbers of migrating salmon were present. Floaters were present, but at much lower densities, throughout the river between Longview and McNary Dam in July of both years—probably as a result of rapid downstream dispersion from points of occurrence of high mortality during this high-flow period.

Most flights were at times when no experimental dead chinook salmon (released by us) were in the river. Only on the flights of September 9, 1954, and July 9, 1955, could experimental fish have been present; six were seen below Bonneville Dam on the first date and four on the second.

The observations on the flights of July 14 and 15, 1955 (fig. 5), were of particular significance because they included the greatest length of river of any surveys and were made during the period of our experiment to estimate chinook salmon mortality. Visibility was good on both days, and we believed our observations revealed typical distribution of floaters at high riverflows. The fact that floaters were most numerous below Bonneville Dam suggests that dead fish were originating near the dam. In the lowest 225 km. of the Snake River, where there were no dams, only three floaters were seen, despite the presence of large numbers of live sockeye and chinook salmon that were migrating up the river.

The aerial surveys were useful in showing that floaters were usually more numerous below Bonneville Dam than in other areas and in indicating the times when the greatest numbers of floaters were present.

MARK-AND-RECOVERY EXPERIMENTS TO ESTIMATE ABUNDANCE OF DEAD CHINOOK SALMON

In the mark-and-recovery technique we used to measure mortality of chinook salmon near Bonneville Dam during periods of high flow, carcasses were tagged and introduced into the river at the dam in 1954 and 1955. The recovery sample consisted of the floaters found on boat searches downstream from the dam at the search stations shown in figure 3. The sample contained the tagged carcasses as well as the carcasses of chinook salmon that died naturally in the river. Only the 1955 experiment had enough recoveries for us to estimate the numbers of dead chinook salmon.

Our experiments differed from an experiment that would lead to a standard Petersen-type of population estimate in one important respect: Instead of removing carcasses from the river,

tagging them, and returning them to the river, we acquired carcasses from other sources, tagged them, and added them to the population of carcasses already in the river.

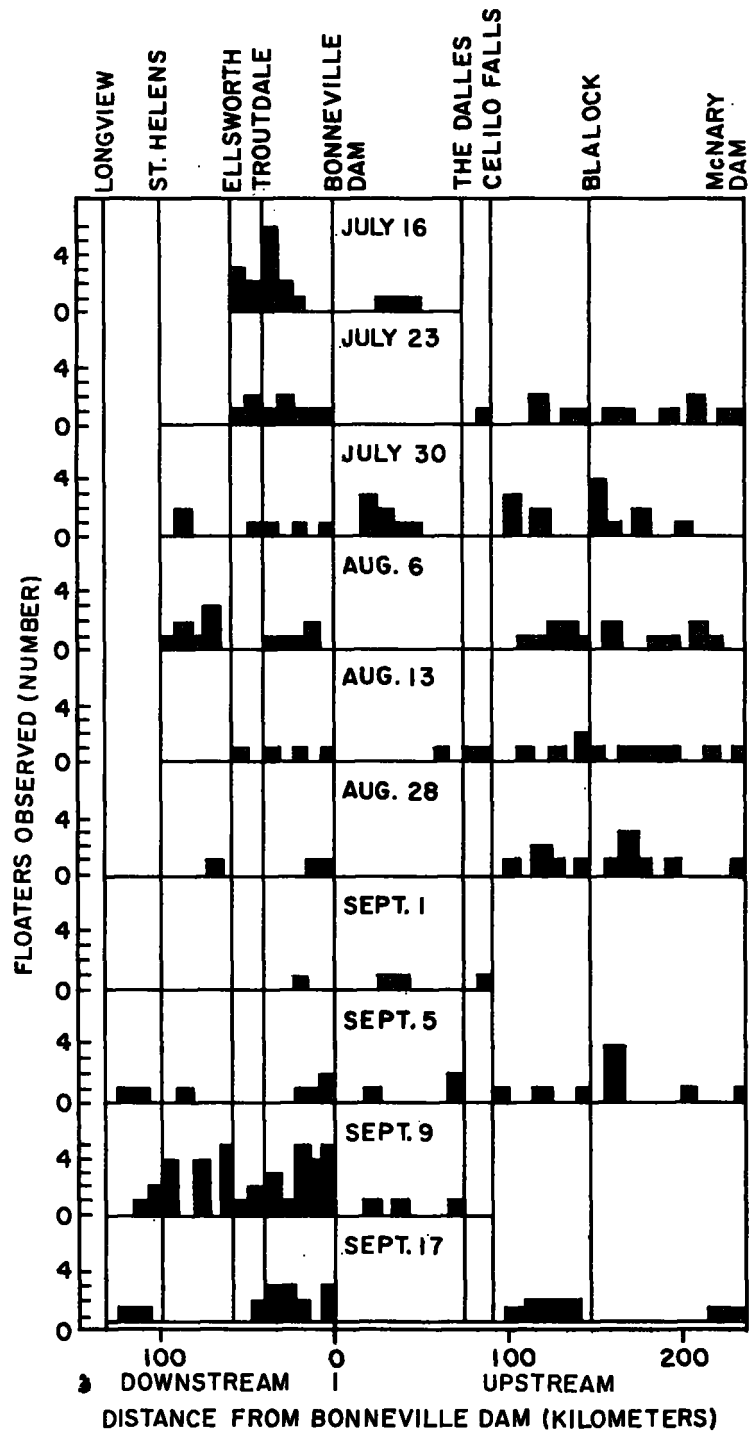

FIGURE 4.—Distribution of floaters observed in 8-km. sections of Columbia River between Longview, Wash., and McNary Dam (320 km.), July 16 to September 17, 1954.

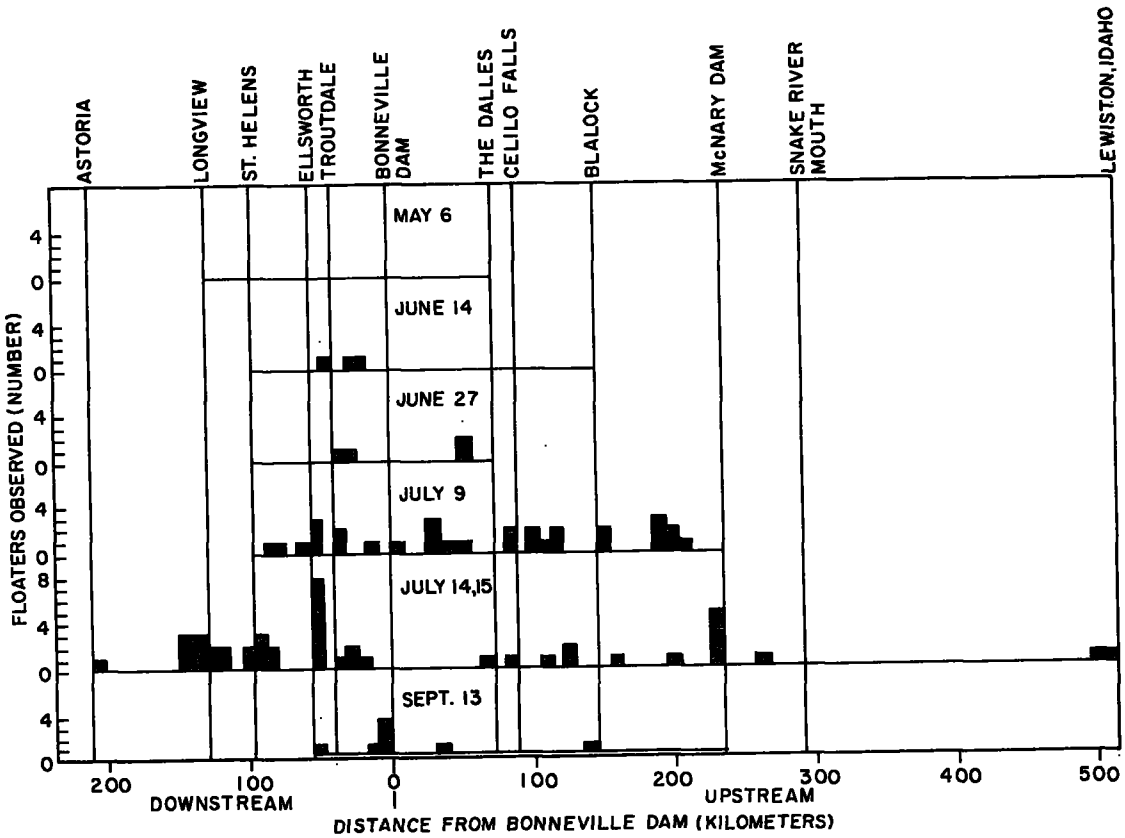

FIGURE 5.—Distribution of floaters observed in 8-km. sections from the mouth of Columbia River, Astoria, Oreg., to its confluence with the Snake River and up the Snake River to Lewiston, Idaho (720 km.), May 6 to September 13, 1955.

It is a simple matter to modify the standard Petersen-type of estimate to fit the circumstances of our experiment, as is shown below. But first, it is instructive to identify our experiment as a typical example of a much larger class of CIR (change-in-ratio) experimental techniques (Paulik and Robson, 1969).

CIR experiments are designed to estimate population characteristics, such as abundance, productivity, rate of exploitation, and survival and mortality rates. Any CIR estimate is based on the observed differences in the relative numbers of two distinguishable types of individuals at two points in time when the population is observed. In our experiment the two types of carcasses are those that are marked (x-type individuals) and those that are unmarked (y-type individuals); the first observation of the population is made immediately before tagging (time 1), and the second observation is made at time of recovery (time 2).

Throughout the following analysis an important distinction is made between carcasses (both tagged and untagged) that are potentially recoverable at the time of death and carcasses that are unrecoverable at the time of death. These two classes of carcasses are mutually exclusive. A potentially recoverable carcass is a more or less unmutilated carcass of a fish that sinks to the bottom of the river after it dies. After several days, it may or may not float to the surface and drift through the area in which recovery crews are searching. Some recoverable carcasses do not float because they are buried or wedged on the bottom, eaten by scavengers, stranded on the bank, or otherwise prevented from floating (these carcasses are still considered recoverable). An unrecoverable carcass is the carcass of a fish so severely mutilated at the time of death that it cannot float to the surface and be recovered. Thus, a recoverable carcass has a fixed chance of floating to the surface where it

can be recovered, whereas an unrecoverable carcass has no chance of floating to the surface. (All floating salmonid carcasses are considered here as floaters.)

We follow Paulik and Robson (1969) in introducing the following notation:

Y_1 = number of untagged recoverable carcasses at time 1. (We wish to estimate Y_1. In our estimate based on 1955 data, this quantity is interpreted as the number of recoverable carcasses below Bonneville Dam resulting from earlier mortalities that could possibly be recovered during our sampling period.)

N_1 = number of tagged and untagged recoverable carcasses combined at time 1.

p_1 = fraction of marked recoverable carcasses at time 1.

p_2 = fraction of marked recoverable carcasses at time 2.

R_x = change in population of marked recoverable carcasses between time 1 and time 2 (i.e., the number of tagged carcasses introduced into the river because it is reasonably assumed that all marked carcasses are recoverable).

R = change in total population of marked and unmarked recoverable carcasses between time 1 and time 2.

n_2 = number of carcasses observed in a sample at time 2.

x_2 = number of marked carcasses observed in a sample at time 2.

$\hat{p}_2 = x_2/n_2$ = estimate of p_2.

The fraction of marked recoverable carcasses at time 2 can be written as the ratio of the number of these carcasses at time 1 corrected for changes that have taken place between times 1 and 2 to the total number of tagged and untagged recoverable carcasses at time 2. That is,

$$\hat{p}_2 = \frac{p_1 N_1 + R_x}{N_1 + R} \tag{1}$$

Solving (1) for N_1 gives

$$N_1 = \frac{R_x - p_2 R}{p_2 - p_1} \tag{2}$$

Because in our experiment there was no change in the population of unmarked recoverable carcasses, $R = R_x$, and because the population consisted entirely of unmarked recoverable carcasses at time 1, $N_1 = Y_1$ and $p_1 = 0$. Substituting these quantities and replacing unknown quantities with their estimates, we arrive at an equation for estimating the number of recoverable chinook salmon carcasses that were killed near Bonneville Dam:

$$\hat{Y}_1 = R_x\left(\frac{1}{\hat{p}_2} - 1\right) \tag{3}$$

If all recoverable carcasses, marked and unmarked, are equally likely to be included in the recovery sample and if the recovery sampling is with replacement (as it was), then it is appropriate to make use of binomial sampling theory to set a confidence interval about $\hat{Y}_1$. To do this, upper and lower limits are set on p_2 (the proportion of marked carcasses in the recovery sample (Pearson and Hartley, 1966)), and these limits are then converted to upper and lower limits for $\hat{Y}_1$ by substituting in equation (3).

As was noted above, this same result can be developed from a Petersen-type estimate by noting that the total number of recoverable carcasses at time of release is $\hat{Y}_1 + R_x$; the number tagged is R_x; the size of the recovery sample is n_2; and the number of recoveries is x_2. Hence,

$$\hat{Y}_1 + R_x = \frac{R_x n_2}{x_2} \tag{4}$$

When solved for $\hat{Y}_1$, this yields expression (3) above.

The validity of this method for estimating the number of recoverable carcasses in the river below Bonneville Dam depends on several basic assumptions. First, we assume that carcasses of untagged chinook salmon float and are similar in all other significant respects to the tagged carcasses we introduced into the river. With regard to floating qualities, we demonstrated the validity of this assumption experimentally by using fresh and frozen chinook salmon carcasses. (These experiments are described in the appendix.) Differences in floating characteristics were insignificant at water temperatures similar to those at the time of our 1955 experiment.

Broadly interpreted, the above assumption implies that all of the untagged carcasses were of fish that had died near the dam; our extensive observations substantiate this implication. In the fall of 1954, when riverflow was low and carcasses were unlikely to be swept far downstream after death before becoming sufficiently buoyant to

float, most carcasses were found within a few miles downstream from the dam. In the summer of 1955, many fresh dead salmon were found on the bottom in shallow water on gravel bars immediately below the dam. Finally, very few floating carcasses were observed during aerial surveys of the forebay above the dam. (See also the data on p. 15, last paragraph.)

Another assumption is that no tags were lost from recoverable carcasses. This assumption is supported by the fact that there was no evidence of missing tags on untagged chinook salmon floaters. The tags were fastened to the jaw in 1954 and to the caudal peduncle in 1955; both locations are exceptionally secure anchoring points for tags on dead salmon.

1954 EXPERIMENT

To secure carcasses for releases in 1954, 1,095 chinook salmon were placed in frozen storage in the summer and fall of 1953. All were ice glazed to retard dehydration and oxidation. About 245 of these fish were spring chinook salmon of both sexes that had been killed during construction of Lookout Point Dam on the Middle Fork of the Willamette River; the rest were fall male chinook salmon from Bonneville and Oxbow Hatcheries on the Columbia River.

Frozen chinook salmon float when placed in water; to ensure that they would sink like a naturally killed salmon, the frozen carcasses were thawed in air for 24 hours before being tagged and released. The tags were sequentially numbered, bright-colored nylon or plastic ribbons fastened to the jaw. The tagged carcasses were released during two periods: The first group (280 carcasses) was released August 4 to 6 when spillway flows averaged 3,300 c.m.s. and powerhouse flows 4,100 c.m.s.; the second group (815 carcasses) was released September 2 to 3 when spillway flows averaged 1,300 c.m.s. and powerhouse flows 3,700 c.m.s.

Earlier evidence suggested that the spillway channel was the source of most dead salmon near the dam. Therefore, most of the tagged carcasses (240 in August and 635 in September) were released into the spillway channel either by dropping them from the dam immediately above the gates or into the rollback below the gates (fig. 2). Another 150 carcasses (20 in August and 130 in September) were dropped into the draft tube discharge at the downstream face of the powerhouse. Finally, 50 were dropped into the river in September from the Bridge of The Gods, 8 km. above the dam, and 20 were released in August from a boat at Oneonta, 11 km. below the dam.

Less than 1 percent of the 1,095 carcasses were recovered. Only one of the 280 carcasses released in August was recovered; it was found at Oneonta on August 10 at the same location where it had been released on August 5. Eight carcasses were recovered from the 815 released in September—six from the powerhouse and two from the spillway releases. No carcasses were recovered from the group dropped from the Bridge of The Gods.

The significance of the apparent difference in the rates of recovery of the carcasses released at the two sites in September can be evaluated by a chi-square test for homogeneity. The null hypothesis is that the probability of a carcass being recovered does not depend on release location. To test this hypothesis, we constructed the following fourfold contingency table:

	Powerhouse release site	Spillway release site	Total
Recovered	6	2	8
Unrecovered	124	633	757
Total releases	130	635	765

For these data, $\chi^2 = 15.35$ with 1 d.f., and the hypothesis of homogeneity is strongly rejected. (The observed frequency for recoveries from spillway releases is smaller than is generally considered desirable for this statistical treatment, but in this experiment the conclusion is so clear-cut that we need not be greatly concerned over this fact.) The conclusion is that carcasses released in the spillway are less likely to be recovered than carcasses released at the powerhouse.

The small number of carcasses recovered from the spillway release indicated that many of them had probably disintegrated in the extremely turbulent flow of the spillway rollback (fig. 2). Such carcasses would have a reduced chance of floating and being recovered. The less turbulent flow of the powerhouse discharge probably contributed to the higher recovery rate of carcasses released there.

Although the 1954 experiment did not produce adequate data to estimate precisely the number

of recoverable carcasses, we can, if we assume that all carcasses released in the powerhouse channel were recoverable, make a crude estimate of the fraction of recoverable carcasses from the spillway releases.

If none of the carcasses released at the spillway had been rendered unrecoverable, the proportion of recoveries from the spillway releases should have equaled the proportion of recoveries from the powerhouse releases. On this assumption, the expected number of recoveries from spillway releases is $\frac{(635)(6)}{130} = 29.3$. Because only two carcasses were actually recovered, we can estimate that the proportion of recoverable carcasses for fish dying by being swept over the spillway is only $\frac{2}{29.3} = 0.0683$ and that the proportion of unrecoverable carcasses is 0.9317. Because this estimate is based on small numbers of recoveries, however, sampling error could be large.

1955 EXPERIMENT

In 1955, 1,169 carcasses were released. They were all male fall chinook salmon collected in 1954 from Bonneville, OxBow, and Spring Creek Hatcheries. They were killed by a blow on the head and placed in frozen storage a few hours later; as in 1953, the carcasses were ice glazed to retard dehydration and oxidation during overwinter storage.

When the carcasses were removed from storage for the 1955 experiment, they were handled in the same manner as the carcasses for the 1954 experiment except that they were tagged with sequentially numbered cellulose-acetate Petersen disks fastened by nickel pins through the caudal peduncle.

Figure 6 demonstrates the rationale on which our entire 1955 study was based: the number of chinook salmon floaters is an indication of the total number of dead chinook salmon in the river. Few floaters were recovered until late June, when

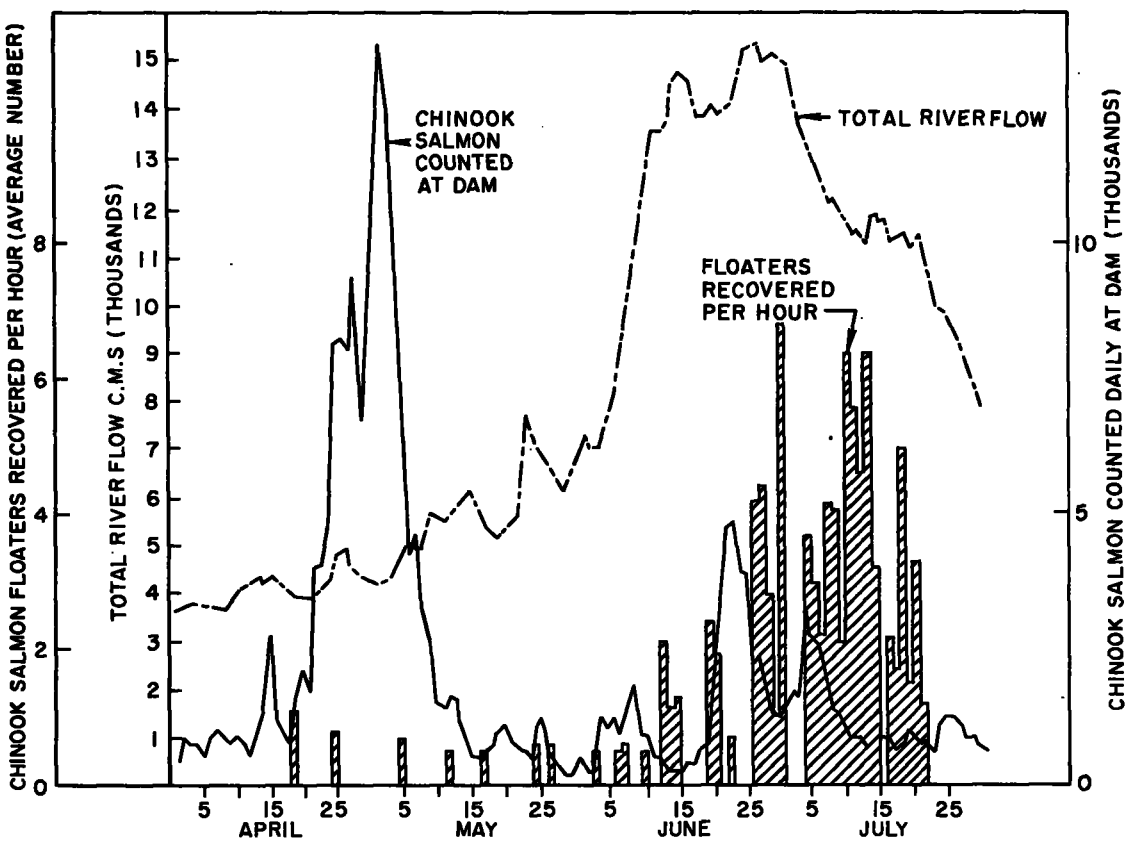

FIGURE 6.—Daily counts of chinook salmon and total riverflow at Bonneville Dam and number of untagged chinook salmon floaters recovered per hour, Bonneville Dam to St. Helens, 1955.

the rate of recovery rose rapidly. We then released our entire supply of carcasses over a 2-day period, June 30 and July 1, so that our estimate of mortality would include a period during which large numbers of salmon were dying. The counts of chinook salmon migrating over the dam and the riverflows were also near their summer maximums. Thus, large numbers of live fish were present, coinciding with inimical high flows.

Because of our experience in 1954 with disintegration of carcasses in the extremely turbulent flow in the spillway rollback, we released the tagged carcasses in 1955 into the spillway channel from a boat downstream from the rollback. In that area high velocities and extreme turbulences shunt migrating salmon toward the fish ladder entrances at either end of the spillway (figs. 1 and 2). At the release points, which were distributed across the river, one man kept the boat in position under power while a second pitched the tagged carcasses overboard—1,068 were released in the spillway channel (183 m. below the dam) and 101 in the powerhouse channel (64 m. below the dam).

The 2-day release period coincided with a temporary slackening of chinook salmon passage over the dam; the count dropped from a peak of 4,912 fish on June 23 to slightly more than 1,000 per day near the end of June. At this time, many live fish were below the dam and were liable to be killed, as shown by a second peak count of 3,434 on July 4 and large numbers of chinook salmon floaters through the first half of July (fig. 6).

The search by boats for floaters downstream from Bonneville Dam was not begun until July 5 because we knew from previous experiments on the floating characteristics of chinook salmon carcasses that the tagged carcasses would not float in fewer than 5 days at the existing water temperature of 13.9° to 14.4° C. (see appendix). Daily searches for floaters continued until July 22. Table 4 gives the release and recovery data on which we base our estimate of the number of recoverable chinook salmon carcasses from mortalities at the dam from June 21 through July 10, 1955. No tagged carcasses were recovered from July 18 through July 22. Table 4 includes only data actually used in computing the estimate.

The level of recovery effort throughout the recovery period was essentially constant—an observer in a boat recovered floaters for 8 hours a day at each of the seven stations below the dam (fig. 3). The only exception was July 16, when no searches were made. This was the 16th day after the releases on June 30 and the 15th day after the releases on July 1; for this reason estimates of fractions of recoverable carcasses available for recovery a given number of days after release (discussed on p. 16) are slightly biased.

The absence of recovery effort on July 16 also affects the estimate of Y_1, the number of recoverable untagged carcasses in the river. However, trial calculations made by using plausible values for the numbers of tagged and untagged carcasses that might have been recovered on July 16 suggest that the likely error is slight. For example, if we assume that one tagged carcass and six untagged carcasses would have been recovered—a probable event in the light of the data of table 4—our estimate of Y_1 (given on p. 17) would change by only 1.8 percent.

TABLE 4.—*Data for computing mortality of the summer chinook salmon run near Bonneville Dam, 1955*

[Only data actually used in computations are included]

Date	Chinook salmon counted at Bonneville Dam ladders	Tagged carcasses released	Tagged floaters recovered from releases of		Untagged floaters recovered
			June 30	July 1	
	Number	*Number*	*Number*	*Number*	*Number*
June:					
21	3,567				
22	4,798				
23	4,912				
24	3,890				
25	3,868				
26	2,220				
27	2,343				
28	1,680				
29	1,291				
30	1,185	338			
July:					
1	1,411	831			
2	1,713				
3	1,667				
4	3,434				
5	2,729		0	0	
6	2,576		0	0	
7	1,940		0	0	8
8	1,339		3	4	15
9	1,241		5	7	13
10	962		0	0	7
11			1	0	13
12			4	4	19
13			0	0	15
14			0	1	16
15			0	1	9
16					
17			0	1	2
18			0	0	
19			0	0	
20			0	0	
21			0	0	
22			0	0	
Total	48,766	1,169	13	18	117

Another minor problem was the removal of untagged carcasses (either floating or stranded in shallow water alongshore) from the river by

sturgeon fishermen. Putrefied salmon flesh is regarded by many sturgeon fishermen as superior bait, and one of the most productive locations on the Columbia River for sturgeon fishing and for finding putrefied salmon is just below Bonneville Dam.

Beacon Rock Moorage, 6.4 km. below the dam, is the principal base of operations for sturgeon fishermen in the area. Lee Motley, a moorage operator, recorded carcasses found by his employees and customers near the dam during the spring and summer of 1955. His data are as follows:

Search period	Chinook salmon		Sockeye salmon	Steelhead trout
	Untagged	Tagged		
April	1			
May	3			
June	29			4
July	48	3	39	3

Of the carcasses found by sturgeon fishermen in July, a relatively large number were found during the sampling period, July 7 to 17 (23 untagged and three tagged chinook salmon and 24 sockeye salmon). This record probably includes most of the carcasses removed by fishermen in the study area.

The numbers of carcasses found by sturgeon fishermen increased steadily during the summer. The relatively large number of carcasses of both chinook and sockeye salmon in July is of particular significance in relation to mortality at the dam. Many of these were not floating but were freshly killed fish that had collected on a shallow submerged bar near the upper end of Hamilton Island, close to the spillway. Each year Lee Motley retrieves many fish on this bar.

Some carcasses recovered by sturgeon fishermen probably would have been found at our regular search stations had they not been intercepted. The fishermen returned the three tagged carcasses to the river because they knew of our study and did not want to interfere with it; two tagged chinook salmon floaters were subsequently recovered at station 6 (fig. 3). The removal of 23 untagged chinook salmon carcasses by moorage personnel during the period of the experiment results in a slightly smaller estimate of mortality than would have been obtained if a few of the removed untagged carcasses had been recovered at search stations. If these were typical recoverable carcasses, a correction for the resulting bias could readily be made by the method suggested by Paulik and Robson (1969). However, carcasses removed by fishermen probably have a higher probability of floating than typical recoverable carcasses, so that a bias correction is not possible. In any event, the bias is very slight and does not significantly affect our conclusions.

The removal of carcasses by scavengers was also considered. Scavengers near Bonneville Dam that feed on dead salmon both before and after they float include sturgeon, squawfish, gulls, crows, raccoons, and skunks. Sometimes almost every floater was accompanied by one gull or more, but at other times, only a few were accompanied by gulls. The effect (if any) of gull scavenging on the length of time carcasses remain at the surface was not determined. Floaters that go aground probably disappear more quickly than those that remain afloat because they are more accessible to terrestrial or avian scavengers. Gulls and crows were frequently seen feeding on dead salmon that had drifted ashore. Nocturnal feeding by raccoons and skunks, which are numerous in the area, may be even more important in the rate of disappearance of carcasses along the riverbanks.

Hence, scavengers reduce to an unknown extent the number of dead salmon available to be observed. Whatever effect scavengers might have had, there was no evidence that it was different for tagged and untagged carcasses in the search area. Therefore, scavenging was assumed to have no significant effect on the estimate of mortality.

Floaters originating above the dam could also affect our mortality estimate, but we believe that few, if any, such chinook salmon floaters drifted into the recovery area during the estimate period. The best and most direct way to evaluate the possibility of recruitment of floaters originating above the dam into the search area below the dam would be to observe the river from above the dam. We looked for floaters on two dates from the Bridge of The Gods, which spans the river 4.8 km. above the dam, where the entire surface can easily be seen. No chinook salmon floaters were observed passing under the bridge on July 10, 1955, whereas seven were sighted below the dam. Again, on July 3, 1956, observers were stationed at station 5 (Cape Horn), and on the Bridge of The Gods. In 6 hours and 35 minutes no chinook

salmon floaters were seen from the bridge, but five were found in 1 hour and 50 minutes at station 5 below the dam. Furthermore, during the period of our study in both 1954 and 1955, greater numbers of floaters were usually found in the 48 km. of river below Bonneville Dam than in any other section of river. No adjustment in the calculated mortality appears necessary for recruitment of untagged floaters into the sample area from above the dam.

The 31 tagged floaters used in the mortality estimates were recovered by our search crews below the dam from July 8 to 17 (table 4). The first tagged floater was found by a fisherman on July 7, the 7th day after the first date carcasses were released (June 30); but it, as well as three other carcasses found by fishermen, was not used in computing the mortality estimate. Our searchers actually recovered 32 tagged floaters, but one was eliminated from the computations because it was on shore.

No tagged floaters were recovered by search crews after July 17, although sampling continued through July 22 (table 4). Because no tagged fish were recovered before July 7 or after July 17, we assume that tagged carcasses were available for recovery only during the period July 7 to 17. During this 11-day period, 117 untagged chinook salmon floaters were recovered at search stations.

The tagged chinook salmon floaters were recovered from 7 to 16 days after they were released (table 5). Because tagged and untagged carcasses behave in a similar fashion, the smoothed daily percentages of total tags recovered given in table 5 can be interpreted to mean that 21.99 percent of the recoverable carcasses of chinook salmon dying on a given day will have a chance of floating and becoming available for recovery on the 7th day after death (of this 21.99 percent, some will actually float and others will not); 19.87 percent will have a chance of becoming available for recovery on the 8th day; 15.71 percent on the 9th day; and so forth. Note that an additional assumption is being made here: An individual floating carcass is available for recovery only on the day that it floats because it drifts out of the recovery area in less than 1 day. This assumption is supported by experiments in which chinook salmon floaters were tagged and later recovered (see appendix). These experiments showed that floaters rapidly passed through the entire recovery area within a few hours during high riverflows.

TABLE 5.—*Number and percentage of 31 tagged chinook salmon floaters recovered below Bonneville Dam on each day after release, 1955*

Days after release	Tagged floaters recovered	Total tagged floaters recovered on each day after release	
Number	*Number*	*Percent*	*Percent smoothed by threes*
7	4	12.90	21.99
8	[1] 10	32.26	19.87
9	[1] 5	16.13	15.71
10	0	0.00	10.46
11	5	16.13	9.43
12	4	12.90	10.46
13	1	3.23	6.28
14	1	3.23	2.10
15	0	0.00	2.10
16	1	3.23	1.57

[1] Two recoveries on July 9 were arbitrarily assigned to releases of June 30 and July 1 because the release dates were unknown.

Knowledge of the estimated percentage of recoverable carcasses that have a chance of floating and becoming available for recovery any given number of days after death (table 5) enables us to estimate the percentage of recoverable carcasses of fish dying on any given date that have a chance of floating and becoming available for recovery at some time during the July 7 to 17 recovery period. The method for calculation of these estimates is shown in figure 7 which, together with table 4, indicates the structure of the 1955 experiment. The figure shows that, of the recoverable carcasses of chinook salmon dying on June 21, an estimated 1.57 percent were recoverable 16 days later on July 7, the first day of the recovery period. Similarly, considering recoverable carcasses from mortalities on June 22, 2.10 percent were recoverable 15 days later on July 7 and 1.57 percent 16 days later on July 8; consequently, a total of 3.67 percent of the carcasses from June 22 mortalities were recoverable during the recovery period. Computations for other days through July 10 follow the same pattern.

We are now ready to estimate Y_1, the number of untagged recoverable carcasses in the river during the July 7 to 17 recovery period. As has been noted, of 1,169 carcasses tagged and released on June 30 and July 1, 31 were recovered floating during the recovery period. At the same time, 117 untagged floating chinook salmon carcasses were observed (table 4). Assuming that all tagged carcasses are recoverable, $R_x = 1,169$,

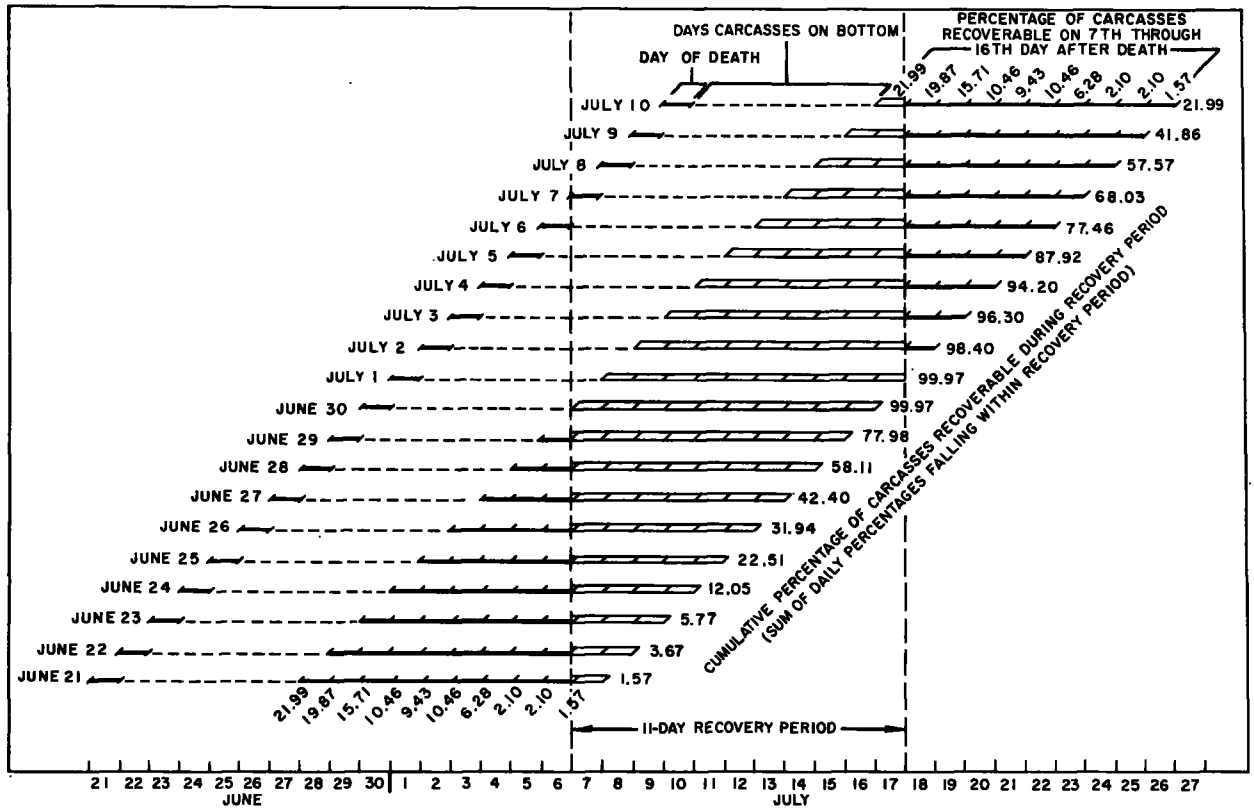

FIGURE 7.—Availability of carcasses for recovery. When chinook salmon die, the carcasses sink to the bottom. Recoverable carcasses may or may not float to the surface between 7 and 16 days after death. When a carcass floats, it can be recovered only on the day it floats. Percentages of recoverable carcasses that become recoverable on the 7th through 16th days after death are given at the top of the figure, and the sums of these percentages falling within the 11-day recovery period are given on the right diagonal edge for each date of mortality.

$x_2 = 31$, $n_2 = 117 + 31 = 148$, and $\hat{p}_2 = 31/148 = 0.2095$. Substituting in equation (3) gives an estimate of Y_1:

$$\hat{Y}_1 = R_x\left(\frac{1}{\hat{p}_2} - 1\right) = 1{,}169\left(\frac{1}{0.2905} - 1\right) = 4{,}412$$

untagged recoverable carcasses. An approximate 95-percent confidence interval on $\hat{p}_2$ is $0.12 \leq 0.2095 \leq 0.33$. The corresponding 95-percent confidence interval on $\hat{Y}_1$ is $2{,}373 \leq 4{,}412 \leq 8{,}572$ untagged recoverable carcasses.

It is clear from the preceding discussion and from figure 7 that this estimate of 4,412 untagged recoverable chinook salmon carcasses represents:

(1.57 percent of the recoverable carcasses from June 21 mortality)
+ (3.67 percent of the recoverable carcasses from June 22 mortality)
+ . . . + (21.99 percent of the recoverable carcasses from July 10 mortality).

PROPORTION OF CHINOOK SALMON RUN KILLED

To estimate the proportion of the chinook salmon run killed near Bonneville Dam during our experiment in 1955, we relate our estimate of the number of recoverable carcasses in the river below the dam (i.e., $\hat{Y}_1 = 4{,}412$ recoverable carcasses) to the size of the run producing these carcasses.

Two additional factors should be taken into account. In our 1955 experiment, all tagged carcasses were released immediately below the dam. This situation would correspond to one in which all chinook salmon mortality at the dam occurs before the fish are counted over the dam. However,

earlier tagging experiments in which salmon were tagged as they emerged from the ladders above the dam showed that some salmon are swept down over the dam and are caught by fishermen below or counted as they reascend the ladders (Schoning and Johnson, 1956). Some of the salmon that are swept over the dam probably do not survive, although we have no direct evidence of what portion is killed. The mortality model that we have developed provides for the possibility that some of the salmon counted over the dam are subsequently killed by being swept back over the dam.

We have evidence from our 1954 experiments (previously described) that carcasses of fish killed by being swept over the spillway may be so severely mutilated by the extreme turbulence that they are rendered unrecoverable. Thus, the second additional factor taken into account in our mortality model is the possible presence of unrecoverable carcasses from mortality occurring after counting.

To derive the mortality model, some additional symbolism is required. In these symbols, the subscript i refers to days on which mortality occurs that could possibly produce floating carcasses for recovery during the recovery period. (Recall that recoverable carcasses may float and be available for recovery 7, 8, . . . , or 16 days after death.) Thus, i = 1 corresponds to June 21 because this is the first day which could have produced floating carcasses for recovery during the recovery period. (The first day of the recovery period, July 7, is the 16th day after June 21.) Similarly, i = 20 corresponds to July 10, the last day which could have produced floating carcasses for recovery during the recovery period. (The last day of the recovery period, July 17, is the 7th day after July 10.) Reference to figure 7 will help to clarify this subscripting scheme.

M = proportion of the chinook salmon run dying near Bonneville Dam. (M is the quantity to be estimated. If the proportion of the run dying at Bonneville Dam remained constant from June 21 through July 10, then M is this quantity. However, if the proportion dying varied during this period, M can be thought of as a weighted average of the daily proportions dying, with the weighting being related to the extent to which carcasses from a given day's mortality become available for recovery during the July 7 to 17 recovery period.)

C_i = count over fish ladders on day i.

D_i = mortalities on day i below the dam.

q_i = proportion of total mortality on day i producing carcasses which, if recoverable, could be recovered during the July 7 to 17 recovery period.

Note that $C_i + D_i$ is the total run on day i and that $M(C_i + D_i)q_i$ is the total number of mortalities on day i producing carcasses, which, if recoverable, could be recovered during the recovery period. Therefore,

$$\sum_{i=1}^{20} M(C_i + D_i)q_i = M\left(\sum_{i=1}^{20} C_i q_i + \sum_{i=1}^{20} D_i q_i\right) \quad (5)$$

is an expression for the total number of mortalities producing carcasses (both recoverable and unrecoverable) which, if recoverable, could be recovered during the recovery period. For 1955, the term $\sum_{i=1}^{20} C_i q_i$ can be estimated from our experimental data and the observed fish ladder counts at Bonneville Dam. Table 6 shows this calculation.

TABLE 6.—*Estimation of* $\sum_{i=1}^{20} C_i q_i$ *for 1955 experiment at Bonneville Dam*

Date	i	C_i (see table 4)	q_i (see table 5)	$C_i q_i$
June:				
21	1	3,567	0.0157	56.0
22	2	4,798	.0367	176.1
23	3	4,912	.0577	283.4
24	4	3,890	.1205	468.7
25	5	3,868	.2251	870.7
26	6	2,230	.3194	709.1
27	7	2,343	.4240	993.4
28	8	1,680	.5811	976.2
29	9	1,291	.7798	1,006.7
30	10	1,185	.9997	1,184.6
July:				
1	11	1,411	.9997	1,410.6
2	12	1,713	.9840	1,685.6
3	13	1,667	.9630	1,605.3
4	14	3,434	.9420	3,234.8
5	15	2,729	.8792	2,399.3
6	16	2,576	.7746	1,995.4
7	17	1,940	.6803	1,319.8
8	18	1,339	.5757	770.9
9	19	1,241	.4186	519.5
10	20	962	.2199	211.5
			Estimate of $\sum_{i=1}^{20} C_i q_i$	= 21,877.6

We now define the quantities required to take account of (1) deaths that occur after counting and (2) the possibility that some of the carcasses

of fish dying after counting are mutilated and rendered unrecoverable.

f_a = fraction of all deaths occurring after counting.

r_a = fraction of carcasses of fish dying after counting that are recoverable (i.e., not mutilated and rendered unrecoverable).

D_o = number of carcasses of fish dying after counting that are unrecoverable.

M_a = proportion of those fish that are counted over the dam that die near the dam.

The quantity D_o can be expressed as

$$D_o = (1 - r_a)f_aM\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right) \quad (6)$$

Because Y_1 is the number of untagged recoverable carcasses in the river, it is clear that Y_1 is the difference between the total number of untagged carcasses and the number of unrecoverable untagged carcasses:

$$Y_1 = M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right) - D_o$$

$$= [1 - f_a(1 - r_a)]M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right) \quad (7)$$

The quantity $\sum_{i=1}^{20} D_iq_i$ represents the number of mortalities occurring below the dam before counting and can be expressed as the difference between the number of untagged recoverable carcasses and the number of untagged recoverable carcasses dying after counting:

$$\sum_{i=1}^{20} D_iq_i = Y_1 - M_ar_a \sum_{i=1}^{20} C_iq_i \quad (8)$$

(Note that at this point, we are assuming all untagged carcasses originating below the dam are recoverable.) Finally, the total number of mortalities after counting can be expressed as follows:

$$M_a \sum_{i=1}^{20} C_iq_i = f_a(Y_1 + D_o)$$

$$= f_a\left[Y_1 + (1 - r_a)f_aM\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right)\right] \quad (9)$$

To derive an expression for M, (9) is solved for M_a, and this result is substituted into (8). Then (8) is solved for $\sum_{i=1}^{20} D_iq_i$, and the result is substituted into (7). An expression for M is then derived by solving (7). The final result is:

$$M = \frac{Y_1}{\left(\sum_{i=1}^{20} C_iq_i + Y_1\right)\left(1 - f_a\right) + f_ar_a \sum_{i=1}^{20} C_iq_i} \quad (10)$$

If all mortality occurs below the dam ($f_a = 0$), then (10) becomes

$$M = \frac{Y_1}{\sum_{i=1}^{20} C_iq_i + Y_1} \quad (11)$$

This situation corresponds to the manner in which we performed our experiment in 1955 when we released all tagged carcasses below the dam. Recalling that $\hat{Y}_1 = 4{,}412$ untagged recoverable carcasses and that $\sum_{i=1}^{20} C_iq_i$ was estimated to be 21,877.8 fish, we use (11) to calculate $\hat{M} = 0.1678$. In other words, on the assumption that all mortality occurs below the dam, we estimate that 16.78 percent of the chinook salmon run was killed near Bonneville Dam in 1955 at the time of our experiment.

It would be desirable to set a confidence interval about the estimate of mortality level given by equation (11). Unfortunately, this does not seem to be possible. All quantities appearing in equation (11) are subject to sampling error. The variances of the q_i's and the variance of Y_1 could be approximately estimated from our experimental data for 1955, but no estimates are available for the variances of the C_i's—the daily chinook salmon counts over the dam. These counts are known to be inexact and may also be biased. Some of the causes of counting errors are: fish are counted more than once as a result of being swept over the spillway; fish are not counted through the ship navigation lock; and fish are misidentified, especially the smaller salmon with similar appearances such as sockeye salmon and chinook salmon jacks. For example, in 1957, only 9,879 chinook jack salmon were counted over Bonneville Dam, but 13,415 were counted over McNary Dam and 8,402 into Spring Creek Hatchery, between Bonneville and McNary Dams (Junge and Phinney, 1963). Thus, more than twice as many jack salmon

were tabulated above Bonneville Dam as were counted in that year at Bonneville.

In developing the model of chinook salmon mortality at Bonneville Dam expressed in equation (10), we assumed that the carcasses of all fish dying below the dam were recoverable. We also assumed that all tagged carcasses introduced into the river below the dam were recoverable. In the event that these assumptions are unjustified, a somewhat more general mortality model can be used. This more general model provides for the possibility that a certain percentage of carcasses released or dying below the dam become unrecoverable.

To derive this model, we define the following quantities:

r_b = fraction of carcasses of fish dying before counting or released below the dam that are recoverable.

T = number of tagged carcasses introduced into the river below the dam.

D'_o = number of carcasses of fish dying before counting that are unrecoverable.

Note that $R_x = r_bT$ so that a more general equation for estimating Y_1 than equation (3) is

$$\hat{Y}_1 = r_bT\left(\frac{1}{\hat{p}_2} - 1\right) \tag{12}$$

An equation for D'_o that is analogous to equation (6) for D_o can be written

$$D'_o = (1 - r_b)(1 - f_a)M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right) \tag{13}$$

Three relationships analogous to those given in equations (7), (8), and (9), respectively, can then be written as follows:

$$\begin{aligned} Y_1 &= M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right) - D_o - D'_o \\ &= (f_ar_a - f_ar_b + r_b)M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right) \end{aligned} \tag{14}$$

$$r_b\sum_{i=1}^{20} D_iq_i = Y_1 - M_ar_a\sum_{i=1}^{20} C_iq_i \tag{15}$$

$$\begin{aligned} M_a\sum_{i=1}^{20} C_iq_i &= f_a(Y_1 + D_o + D'_o) \\ &= f_a\left[Y_1 + (1 - f_ar_a + f_ar_b - r_b)\right. \\ &\qquad \left. M\left(\sum_{i=1}^{20} C_iq_i + \sum_{i=1}^{20} D_iq_i\right)\right] \end{aligned} \tag{16}$$

Equations (14), (15), and (16) may be used to derive a general expression for M in the same way that equations (7), (8), and (9) were used to derive the expression for M given in equation (10). The result, which allows for the possibility of carcasses of fish dying or being introduced into the river below the dam becoming unrecoverable, is as follows:

$$M = \frac{Y_1}{\left(r_b\sum_{i=1}^{20} C_iq_i + Y_1\right)(1 - f_a) + f_ar_a\sum_{i=1}^{20} C_iq_i} \tag{17}$$

where the value of $\hat{Y}_1$ from (12) is used. Note that equations (12) and (17) reduce to equations (3) and (10), respectively, when $r_b = 1$.

In estimating that 16.78 percent of the chinook salmon run was destroyed near Bonneville Dam, we assumed that all mortalities occurred below the dam (i.e., that $f_a = 0$). As has already been pointed out, it is likely that some mortality occurs as a result of fish being swept back over the spillway after they have been counted. Therefore, it is of considerable interest to explore the effect that this mortality of counted fish would have on our estimate of M. Because some of the carcasses of fish that die by being swept back over the spillway could be so severely mutilated as to be rendered unrecoverable (i.e., have no chance of floating and being recovered), this factor must also be considered.

To explore the various possibilities, f_a (fraction of deaths occurring after counting) and r_a (fraction of carcasses of fish dying after counting that are recoverable) were assumed to take on various pairs of values, and $\hat{M}$ was calculated for each assumed pair of values by using equation (10).

For f_a the following values were assumed: 0.0, 0.125, 0.250, 0.375, 0.500, 0.625, 0.750, 0.875, and 1.0. The same values were assumed for r_a, and $\hat{M}$ was calculated for all possible pairwise combinations of these values. From these results, we constructed an isopleth diagram giving values of M corresponding to values of f_a and r_a (fig. 8).

Figure 8 shows that our estimate, $\hat{M} = 0.1678$ (based on the assumption that $f_a = 0$) is a mini-

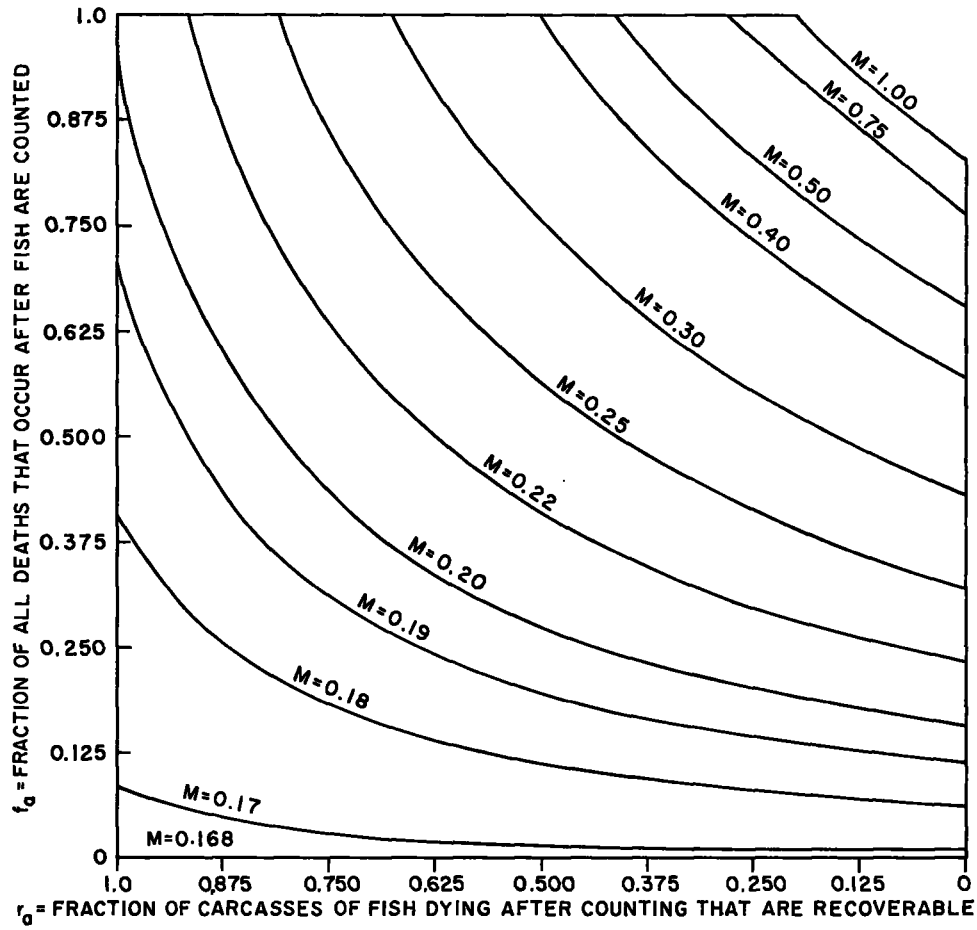

FIGURE 8.—Values of $\hat{M}$, the fraction of the chinook salmon run dying near Bonneville Dam at the time of the 1955 experiments, corresponding to pairs of values for f_a and r_a.

mum point estimate of the level of chinook salmon mortality at Bonneville Dam. As f_a increases, $\hat{M}$ also increases; the rate at which $\hat{M}$ increases depends strongly on the value of r_a. For large values of r_a, corresponding to an assumption that only a small percentage of the carcasses of fish that die by being swept over the spillway are rendered unrecoverable, values of $\hat{M}$ increase only slightly as f_a increases. On the other hand, if a large percentage of these carcasses are rendered unrecoverable, r_a is small and $\hat{M}$ increases rapidly as f_a increases. (Note in figure 8 that points in the region above and to the right of the line for $\hat{M} = 1.00$ correspond to values of f_a and r_a that are incompatible with data collected in our 1955 experiment.)

FACTORS ASSOCIATED WITH MORTALITY AND THEIR SIGNIFICANCE

We have established in preceding sections that many chinook salmon died near Bonneville Dam at the time of our 1955 experiment. The next logical step is to examine factors associated with these deaths to determine the actual cause or causes.

In addition to the 1955 period, we also examined available information for other periods between 1943 and 1956 when high or low mortality was apparent (table 7). The seven periods of apparently high mortality were September 1943, September 1950, May 1952, July 1954, September 1954, June-July 1955, and June-July 1956. Low mortality periods were September 1946 and April-May 1955.

TABLE 7.—*Comparative mortality of chinook salmon at Bonneville Dam in spring, summer, and fall periods between 1943 and 1956*

Season and date	Average daily spillway flow	Water temperature range	Average count of chinook salmon at dam	Search time	Chinook salmon floaters	Chinook salmon floaters per hour of search	Chinook salmon floaters per hour per 10,000 fish	Mortality rating
	C.m.s.	*° C.*	*Number*	*Hours*	*Number*	*Number*	*Number*	
Spring:								
May 1–31, 1952	8,700	11.1–13.9	3,478	----------	(1)	----------	----------	High
April 20 to May 10, 1955	1,050	7.8–11.1	6,481	212.6	2	0.009	0.015	Low
Summer:								
July 1–31, 1954	7,900	14.4–17.8	1,051	26.5	30	1.132	10.771	High
June 20 to July 22, 1955	9,020	13.9–17.2	1,836	603.4	194	0.322	1.751	Do.
June 20–29, 1956	10,500	13.3–15.6	4,317	6.5	19	2.923	6.771	Do.
Fall:								
Sept. 1–15, 1943	620	18.3–18.9	12,543	8.0	146	18.250	14.550	Do.
Sept. 1–30, 1946	140	16.1–20.6	9,235	116.6	21	0.180	0.195	Low
Sept. 1–20, 1950	480	18.9–20.6	10,054	----------	54	----------	----------	High
Sept. 1–15, 1954	1,160	17.8–18.3	5,001	125.5	99	0.789	1.577	Do.

[1] A commercial fisherman reported "thousands" of dead chinook salmon below the dam.

The "high" and "low" mortality ratings are subjective classifications based on the number of chinook salmon floaters relative to the average daily chinook salmon counts at Bonneville Dam. Major differences in search techniques and in the lengths of search periods make detailed comparison between most of the periods of dubious value. Only for our study in 1955, and for a brief followup study in 1956, can we be certain that search techniques were comparable. We, therefore, gave the greatest weight to data for these years in reaching our conclusions. Data for earlier years were useful, however, in lending support to the conclusions.

In spring 1955, when spillway flows and water temperatures were low and numbers of salmon were high, only 0.009 chinook salmon floater was found per hour of search. Later the same year (midsummer), when spillway flows averaged 9,000 c.m.s., water temperatures were higher, and numbers of salmon were low, 0.322 chinook salmon floater was found per hour of search.

A pattern of characteristic circumstances accompanying high mortality periods was evident: floating dead salmon were likely to be especially numerous below the dam when either high spillway flows or exceptionally large numbers of salmon occurred. If high flows and large numbers of salmon occurred simultaneously, even greater numbers of floating dead salmon could be predicted downstream from the dam. The data in table 7 generally substantiate this conclusion.

After completing our study in 1955, we wished to test the hypothesis that large numbers of chinook salmon would die and float near Bonneville Dam whenever large numbers of fish and high spillway flows coincided. Late June 1956 had such a coincidence.

From June 20 to 29, spillway flow at the dam averaged 10,500 c.m.s. and coincided with chinook salmon counts over the dam averaging over 4,300 per day. We predicted that at the prevailing water temperatures of 13.3° to 15.6° C., floaters from a given day's mortality would appear downriver about 7 days later and a large number of floaters would be evident below the dam by about July 3. On July 3, during 1 hour and 50 minutes of search at the Cape Horn station, five chinook salmon carcasses were observed; on July 5, 14 carcasses were seen during 4 hours and 40 minutes of observation. In terms of numbers of chinook salmon floaters recovered per hour these numbers were greater than for any previous observation period (except September 1943), indicating, as predicted, that serious mortality had occurred. The cause of the high mortality of September 1943 is unknown.

FLOW

We were unable to determine which specific conditions at Bonneville Dam contribute to salmon deaths, but evidence is strong from our study and from observations in earlier years that high mortality in spring and summer occurs during high flows. The annual peak flow of the Columbia River at Bonneville Dam is in May or June, depending on the time of maximum snowmelt in the upper watershed; the peak flow dates from 1938 to 1955 fell between May 11 and June 28. Flows of more than 8,500 c.m.s. may occur for up to 3 months.

The maximum combined flow capacity of the 10 power turbines at Bonneville Dam is about 4,100 c.m.s. when the Columbia River is at flood stage. At low riverflows, maximum turbine capacity is about 3,400 c.m.s. This means that flows

above 4,100 c.m.s. during high water and above 3,400 c.m.s. during low water are discharged through the spillway (flows through the fish ladders are an insignificant portion of the total flow).

Columbia River chinook salmon migrations may be separated into spring, summer, and fall runs by their time of appearance at Bonneville Dam. For the purpose of this discussion, the spring run is defined as occurring in April and May, the summer run in June and July, and the fall run in August and September. Only a few chinook salmon migrate past Bonneville Dam before April or after September.

The three runs are characteristically exposed to different river discharges at the dam. The summer chinook salmon run, the smallest of the three, usually migrates upstream during the period of peak river discharge. Less frequently the spring run passes the dam during annual peak flows, although both spring and summer runs are always subjected to relatively high flows. During the fall run, flows are relatively low and little water is discharged through the spillway.

Figure 9 shows the daily flows at the dam in 1946–55 for the periods when the central 75 percent of the spring, summer, and fall chinook salmon runs were counted. The 75-percent figure was arbitrarily selected to include the major part of each run; 12.5 percent was subtracted from each end of the run to determine the 75-percent period. The dashed line indicates the 7,000-c.m.s. flow level.

The 7,000-c.m.s. figure was arbitrarily selected as the point above which heavy mortalities occur, based primarily on 1955 information—the year for which the most extensive data are available (fig. 6). The reasons for establishing 7,000 c.m.s. as the critical level are: In 1955, 75 percent of the spring run passed the dam when total river flow was low—between 4,200 and 5,100 c.m.s.; few floating chinook salmon were observed on an intensive search of the river during a large spring chinook salmon run (172,000); the maximum daily count past the dam was more than 13,000 fish. Therefore, flows under 5,100 c.m.s. were not associated with a high mortality. Increasing numbers of floating chinook salmon became apparent downriver from the dam by June 12, 1955, after a period when the chinook salmon count was

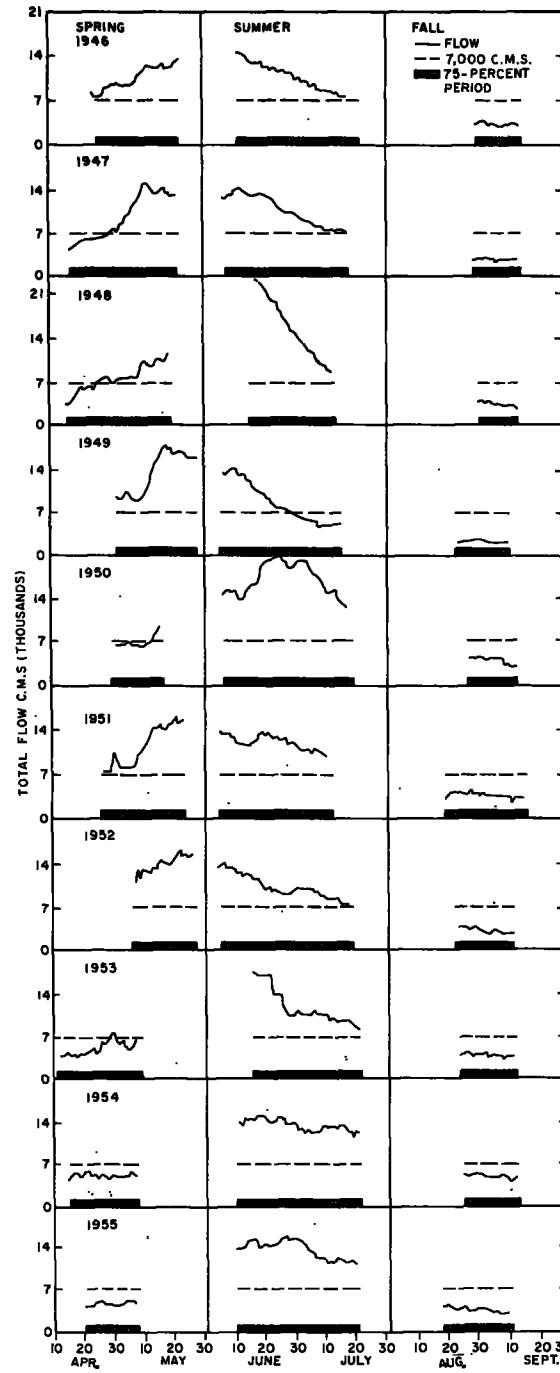

FIGURE 9.—Columbia River flows (solid lines) at Bonneville Dam during periods (horizontal bars) when 75 percent of the spring, summer, and fall chinook salmon runs passed the dam, 1946–55. Dashed line at 7,000 c.m.s. indicates flow above which serious mortality occurs.

about 1,100 fish per day for several days and flow had increased to between 7,000 and 9,900 c.m.s.

To understand better the relation of numbers of chinook salmon counted at the dam and numbers floating below the dam, it should be noted that at a water temperature of 14.4° C., salmon carcasses float in about 7 days after death (appendix table 1). Because water temperature averaged 13.3° C. during the first 10 days of June 1955, 8 or 9 days would elapse between death and the time carcasses first floated. The increase in floaters observed after mid-June was an indicator that after June 3, when total riverflow approximated 7,000 c.m.s., the numbers of chinook salmon dying suddenly increased. We conclude on the basis of these observations that mortality may be expected to be high whenever total riverflow rises above 7,000 c.m.s., and low whenever total flow is less than 5,100 c.m.s.

In some years (1943, 1946, 1950, and 1954) floating chinook salmon were recovered below the dam when total flow was less than 5,100 c.m.s. Although data for these periods are limited, the relatively large numbers of floating chinook salmon in September 1943 and 1950 probably represented a low rate of mortality because very large numbers of chinook salmon were migrating through the area. The search by A. Suomela in 1943 (discussed in an earlier section), which resulted in the recovery of a large number of carcasses, is not comparable with later searches because he searched in midstream, on shore, in eddies, and any place that fish could be expected to accumulate, whereas in our later searches, floaters were observed only from fixed locations. Fall chinook salmon runs in these 4 years of apparently high mortality were large—peak daily counts at Bonneville Dam were 20,000 to 30,000 chinook salmon. Water temperatures were about 21.1° C., and riverflows were low. Under these conditions, floating chinook salmon were more apparent because they floated in a shorter time, thereby reducing their dispersion downstream from the area of death both before and after they became buoyant.

The many floaters below the dam in September 1954 may have represented a higher rate of loss of chinook salmon than is usual in the fall. Daily counts were relatively low; the peak was only about 8,000. During the 75-percent period of passage of the 1954 fall run, total riverflow was the highest in the 10-year period 1946–55, ranging from about 4,700 to 5,500 c.m.s. This higher-than-normal flow may have resulted in a somewhat higher-than-average fall mortality rate.

Because a total flow of 7,000 c.m.s. or greater is associated with high mortality rates, figure 9 may be interpreted as follows: (1) The flow over Bonneville Dam has never reached 7,000 c.m.s. during the fall run of chinook salmon. Observations have substantiated that fall runs generally have experienced relatively low mortality rates. (2) Most of the summer chinook salmon run in every year has been subjected to flows exceeding 7,000 c.m.s., which are associated with a high level of mortality. (3) In 4 of the 10 years (1946, 1949, 1951, and 1952) the entire 75-percent periods of spring runs were subjected to flows greater than 7,000 c.m.s., and in 2 of the remaining 6 years (1947 and 1948) flows exceeded 7,000 c.m.s. for about two-thirds of the 75-percent period. The remaining four spring runs (1950, 1953, 1954, and 1955) passed the dam when flows were less than 7,000 c.m.s.

In summary, fall runs of chinook salmon were never subjected to killing flows; spring runs were exposed to killing flows in some years; and summer runs always encountered killing flows.

WATER TEMPERATURE

River water temperatures affect the floating qualities of carcasses and thereby make carcasses more or less evident to observers. Warm water makes carcasses more apparent and cold water makes them less apparent.

Flotation experiments described in the appendix showed that carcasses require more time to float in cold water than in warm. As a result, in the interval between death and floating, carcasses may be swept farther downstream during periods of low water temperatures than during periods of high temperatures. Furthermore, during the longer interval between death and floating in cold water, scavengers have more opportunity to consume carcasses.

With this in mind, we examined the relation of water temperatures and numbers of chinook salmon counted at the dam. In 1946–55 the range of temperatures during spring runs (April and May) was 7.8° to 13.9° C.; during summer runs (June and July), 10.0° to 19.4° C.; and during fall runs (August and September), 17.8° to 21.1°

C. (fig. 10). Thus, dead salmon are least likely to be evident as floaters in the spring and most likely to be evident in the fall. Figure 10 shows that in the spring of 1955 average water temperatures were the lowest for the 10 years shown (8.9° C.). Unusually cold water probably contributed to the almost complete absence of floaters during the spring run in 1955. In 1952, a period of apparently high mortality (table 7, fig. 10), water temperatures during the spring chinook salmon migration were highest of the 10-year period.

TURBIDITY

Turbid water, as measured by Secchi disk visibility, was investigated as a possible factor contributing to chinook salmon deaths. We hypothesized that fish rely partially on sight to locate and negotiate the fish ladders, and reduction of visibility might handicap them.

High flows in the Columbia River are characterized by turbid water, and low flows by relatively clear water. During low flows the water may be turbid for short periods when a tributary floods from heavy rains or rapid snowmelt. For example, in mid-January 1953 after a flash flood on a tributary, a Secchi disk visibility reading of 0.06 m. was recorded at Bonneville Dam when flow was only 2,700 c.m.s.

Secchi disk visibility at the dam has seldom been less than 0.3 m. during periods of major salmon migrations (fig. 11). From 1950 to 1955, visibility was 0.3 m. or less for only short, infrequent periods from April to September, except in 1952, when it remained about 0.3 m. or less from April 1 through May 30, throughout the spring migration. The 1952 spring run suffered a heavy mortality, but because the high turbidity was accompanied by high flows and relatively high water temperatures, it was impossible to evaluate the separate effects of flow, temperature, and turbidity.

In 1955, from April 10 to June 30, Secchi disk visibility varied between 0.3 and 0.8 m.; it was 0.6 m. at the peak of the spring chinook salmon run (May 2) and 0.45 m. at the peak of the summer run (June 23). Few floating chinook salmon were observed in May, but large numbers were seen in June and July. Because turbidity differed little between the two periods, we concluded that it was not a major factor in mortality at the dam in 1955.

Because high turbidity and high flow usually coincide, we could not evaluate the separate effect of turbidity, if any.

COMMERCIAL FISHING

The Columbia River gill net fishery has sometimes been blamed for dead salmon in the river because some fish escape from nets after becoming enmeshed. An escaped fish usually has characteristic net marks—encircling bands where scales have been scraped off and cuts on the anterior edges of fins. Hanson et al. (1950: 24) concluded from observations in the fish ladders at Bonneville Dam and at hatcheries above and below the dam that "Most injuries to the fish observed are traceables (sic) to fishermen's gill nets; none of the injuries were directly traceable to conditions at Bonneville Dam. Most net injuries were not fatal to fall-run chinook salmon at hatcheries above and below Bonneville Dam in 1946." The conclusion is questionable because only the fish that survived after being injured were available for observation—those that may have died could not, of course, be sampled at the hatcheries.

Most significant in discounting gill nets as a major cause of mortality in our study is the fact that 85,769 spring chinook salmon passed the dam in May 1955 with little apparent mortality, despite an intensive commercial gill net fishery from April 30 to May 27. The spring chinook salmon run during this period was the largest since 1939 (the first year runs were counted at Bonneville Dam). The catch was 80 percent of the total run; the catch below the dam was the second largest since 1939. Four stations below the dam and one station near The Dalles were searched intensively for floaters throughout this period, but few were found and none of these bore characteristic net marks. This is strong evidence against attributing the death of floating chinook salmon to the gill net fishery.

We concluded that gill net injuries are not a major cause of death of chinook salmon found floating near the dam.

FISH PASSAGE FACILITIES AT BONNEVILLE DAM

Great effort has been made by fishery agencies and especially by the U.S. Army Corps of Engineers to discover any structure or operation at the dam that might delay, injure, or kill migrating adult fish. Mechanical failures or routine

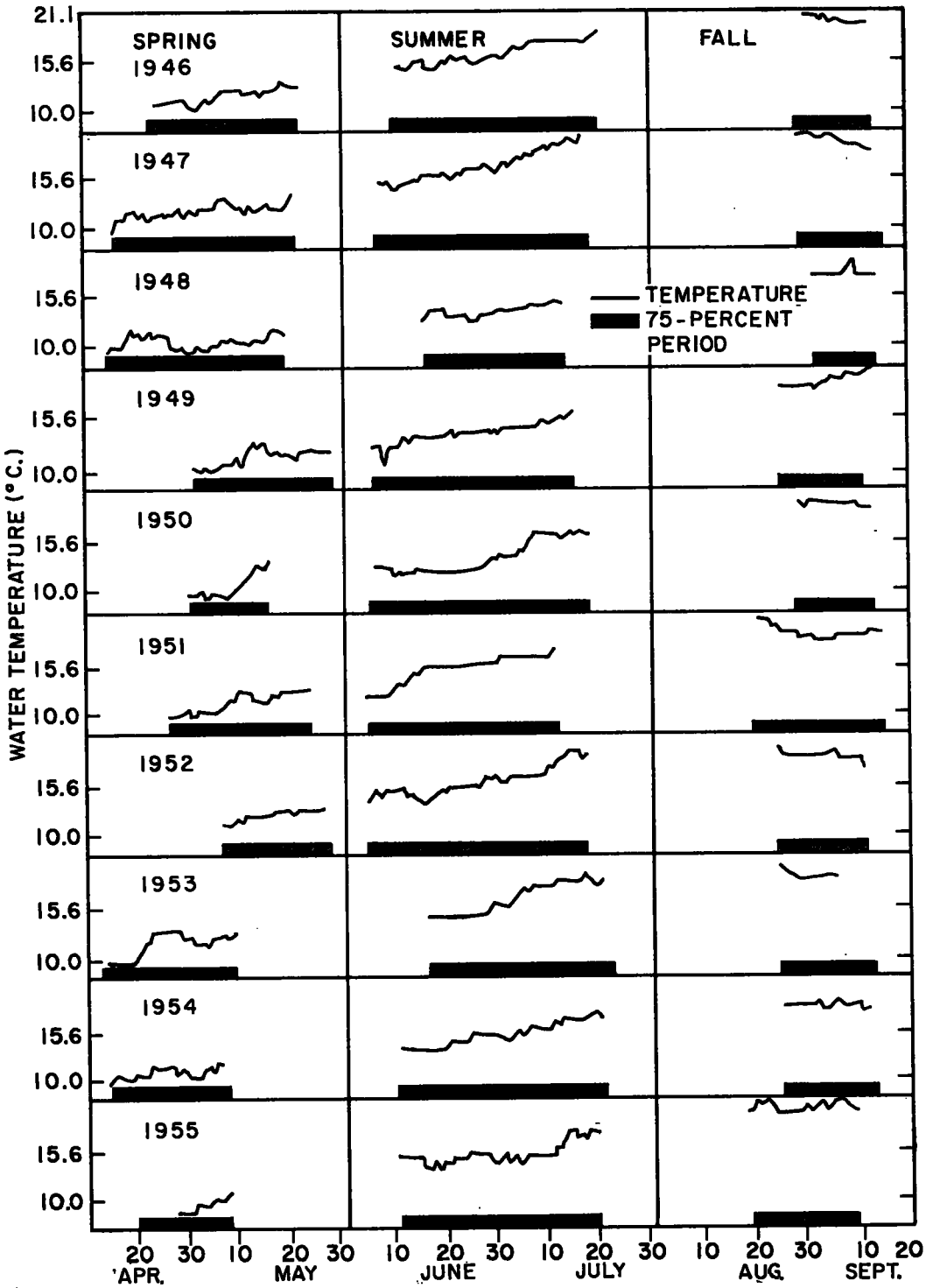

FIGURE 10.—Columbia River water temperatures at Bonneville Dam during periods when 75 percent of the spring, summer, and fall chinook salmon runs passed the dam, 1946–55.

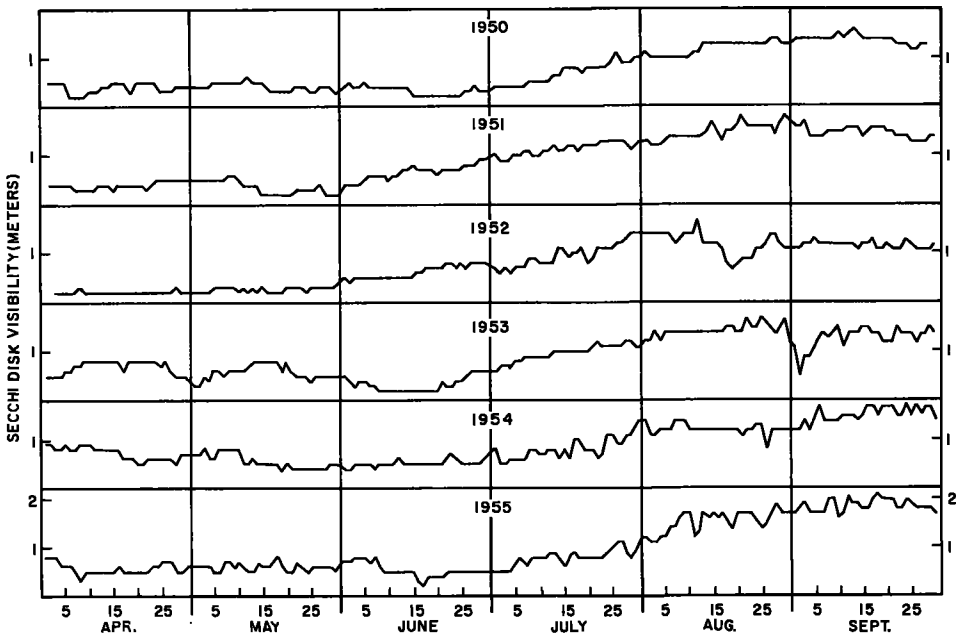

FIGURE 11.—Secchi disk visibility in the Columbia River at Bonneville Dam, 1950–55.

maintenance operations have sometimes necessitated shutting down portions of the fish-passage facilities, but these have rarely affected passage for long.

Many improvements have been made in the fish passage facilities at Bonneville Dam over the years. Among them are alteration of the powerhouse collection system, addition of auxiliary attraction flows at the entrance to the ladders, installation of flow baffles below the ladder entrances, and installation of barrier screens below the spillway bays adjacent to the ladder entrances.

In 1946 a submarine viewing chamber made of a section of large steel pipe with the ends sealed off and with two watertight windows, was used by the U.S. Army Corps of Engineers and FWS. A series of observations of migrating fish were made by an observer inside the chamber, which was lowered into a fish ladder. Fish within the ladder experienced no difficulty in moving through the ladder (Hanson et al., 1950). Other observations through the years have shown that once fish have entered the ladders they generally pass through with little or no injury or delay.

Because there is no evidence that fish are injured in the ladders, we eliminated this possible source of mortality from further consideration.

DISEASE

Another possible cause of salmon mortality is disease. In 1954 and 1955, to determine the causes of death we collected all of the recently killed fish we could find below the dam.

None of the fish collected in 1954 were sufficiently fresh to warrant a detailed examination, although gross injuries of external origin were obvious in some instances (table 8).

In 1955, we recovered three chinook and six sockeye salmon, four white sturgeon, one shad, and two carp in fresh condition (table 8). Seven of the fish (two chinook and five sockeye salmon) were immediately frozen and later autopsied by Edward M. Wood, fish pathologist at the FWS Fish Nutrition Laboratory, Carson, Wash. In summarizing the results of his examinations, Wood said:

> "In some cases these fish had severe injuries which clearly caused death. In these instances we have attempted to determine if there were any contributing factors which might have made the fish more susceptible to injury such as disease. At other times, however, there was no gross evidence of injury other than slight internal hemorrhage, congestion of various organs with blood, or

slight edema over the brain. In these cases we do not know the cause of death and little of the nature of the injury. All of these fish were sexually immature and death was presumably not related to the reproductive cycle."

TABLE 8.—*Observations at time of recovery of 8 moribund and recently dead fish found within 5 miles of Bonneville Dam, 1954–55*

Date found	Species	Condition at time of recovery
1954:		
September 9	Chinook salmon	Fresh; jaw reflexes; right eye turned backward into socket; gills bleeding; slight bloody bruises on pectoral fins, isthmus, right opercle, and caudal peduncle.
September 11	White sturgeon	Fresh; fin reflexes; abrasions on pectoral girdle and side.
1955:		
May 3	do	Alive; deep gash near left ventral fin.
May 12	do	Alive; peduncle severed.
Do	Carp	Alive, deep dorsal gash.
Do	do	Fresh; decapitated.
May 18	White sturgeon	Severed at midbody.
June 7	Chinook salmon	Fresh; torn premaxillary, isthmus, and first gill arch; clotted blood in heart cavity.
June 10	Chinook salmon [1]	Moribund; abrasions on head and dorsal fin; blood clot between first and second left gill arches.
June 17	American shad	Fresh; head severed; caudal peduncle severed.
June 21	White sturgeon	Fresh; body severed.
July 9	Sockeye salmon	Fresh; abrasion on left opercle.
July 12	Sockeye salmon [1]	Fungused gashes on right side.
Do	do	Fresh; no apparent injuries.
Do	do	Do.
July 14	do	Fresh; massive wound into body cavity.
July 15	do	Alive; floating.
July 21	Chinook salmon [1]	Large gash on peduncle.

[1] Autopsy performed.

Since the conclusion of our study of mortality, other investigators have discovered that supersaturation of nitrogen in Columbia River water at times of high flow may be a significant cause of fish mortalities. Some of the physiological symptoms described by Wood when he autopsied the fresh dead salmon are characteristic of nitrogen poisoning (such as internal hemorrhaging and congestion of spleen), which could well have been a direct cause of mortality that we did not recognize.

Ebel (1969) found that nitrogen saturation levels potentially dangerous to fish always occurred at Bonneville Dam when water was discharged through the spillway. Nitrogen supersaturation may occur when atmospheric nitrogen is entrained and dissolved in the plunging turbulent spillway flow. Therefore, highest nitrogen saturation values coincide with peak spillway flows. Nitrogen levels in tail waters below Bonneville Dam were substantially higher than levels below seven other Columbia River dams. High nitrogen levels, coinciding with high flows and a delay of chinook salmon below Bonneville Dam (Schoning and Johnson, 1956) could have been the immediate cause of death of at least a portion of the chinook salmon included in our estimate of mortality.

An epidemic of the bacterial disease columnaris, *Chondrococcus columnaris*, among salmon (particularly sockeye) was reported in the Columbia River system in late July and August 1955.[6] Sockeye salmon in the latter part of the run seemed more heavily infected than those in earlier segments, probably because water temperature increased during the summer. We do not believe that columnaris was an important contributing factor to death of chinook salmon in June and early July 1955 because our study was completed before the outbreak of the disease. Because columnaris epidemics are associated with relatively warm water, mortalities reported during spring cold-temperature periods in previous years were probably not caused by this disease.

In summary, although we were able to recover only a small number of freshly killed fish immediately below Bonneville Dam, there was no indication that disease contributed to death in 1954 and 1955. Many of the fish had severe recent external injuries. Some of the dead fish without massive injuries probably died as a result of nitrogen poisoning, a potential cause of death not recognized by us at the time of our study.

SUMMARY

1. In most years since the completion of Bonneville Dam in 1938, floating dead fish—particularly chinook salmon—have been observed downstream from the dam.

2. In 1954 and 1955 the Oregon Fish Commission, under a contract with FWS, studied salmon mortality at Bonneville Dam.

3. The main aims of the studies were to estimate the chinook salmon mortality at Bonneville Dam and to determine the causes of death.

4. From ratios of tagged to untagged floating carcasses, we estimated that 4,412 recoverable carcasses of chinook salmon that had died near Bonneville Dam were in the river at the time of our 1955 experiment.

5. The chinook salmon mortality at Bonneville

[6] Erling J. Ordal. 1955. Progress Report No. 13, U.S. Fish and Wildlife Service, Contract No. 14-19-008-2418, 7 pp. On file Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash. 98102.

Dam was estimated to be 16.8 percent of the total run during the period of our 1955 experiment (June 21 through July 10).

6. If a substantial proportion of the fish died after they were counted (by being swept back over the spillway) and if a substantial number of these carcasses were mutilated and rendered unrecoverable, actual mortality was substantially higher than our estimate.

7. Our experiment probably included the period of maximum mortality in 1955.

8. The numbers of floating carcasses are related to the amount of flow of the Columbia River. The mortality of salmon is highest when flows exceed 7,000 c.m.s.

9. Fall chinook salmon runs have never been subjected to flows above 7,000 c.m.s. (killing flows); spring runs were exposed to such flows in some years; and summer runs nearly always encountered such flows.

10. Water temperature, turbidity, disease, and injuries from gill nets had little influence on the number of carcasses in the river.

11. The specific causes of death and the precise areas at Bonneville Dam where death occurred were undetermined, but the major source of chinook salmon mortality is associated with the spillway during high flows.

12. We did not consider nitrogen poisoning resulting from high flow turbulence as a possible cause of mortality at the time of our experiment, but evidence subsequently developed by other investigators indicates that this may be a major specific mortality factor.

ACKNOWLEDGMENTS

Fred C. Cleaver, formerly Assistant Director of the Oregon Fish Commission, contributed greatly to the planning and analysis. Ivan J. Donaldson, Resident Biologist, U.S. Army Corps of Engineers, Bonneville Dam, helped release tagged experimental fish and provided information on mortalities of previous years.

John A. Dudman, Associate Professor of Mathematics at Reed College, and Richard F. Link, Assistant Professor of Statistics and Mathematics at Oregon State College, provided technical assistance in the early stages of the statistical analyses.

Lee Motley, operator of Beacon Rock Moorage, supplied information on the use of salmon carcasses by fishermen for sturgeon bait. Finally, Edward M. Wood, former pathologist of the U.S. Fish and Wildlife Service, performed the histological examinations of freshly killed salmon to determine causes of death.

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APPENDIX

EXPERIMENTS ON FLOATING QUALITIES OF CHINOOK SALMON CARCASSES

This appendix describes experiments designed to test two key assumptions: (1) that experi-

mental tagged carcasses and carcasses of natural river-killed fish have similar floating characteristics; (2) that floating carcasses pass rapidly through the recovery area and are available for recovery on only 1 day.

Floating Qualities of Fresh and Experimental Carcasses

Salmon sink after death, but decomposition gases cause them to float after a period of time. In the mark-and-recovery method that we used to estimate the population of dead fish, it was essential to ascertain whether tagged experimental carcasses had floating qualities similar to those of other salmon that die in the Columbia River. Differences between the two kinds of carcasses could influence results. We made a series of experiments at various water temperatures with fresh and frozen experimental chinook salmon carcasses to determine whether there are differences in elapsed time between death and rise of the carcass to the surface.

Some information was already available from experiments by Hanson et al. (1950). They determined the elapsed time between death and floating for 21 fresh salmonids at water temperatures of 13.9° to 20.6° C. We performed similar experiments over a wider range of temperatures with 24 frozen and 14 fresh chinook salmon. Cold-water experiments were done in a spring-fed pond at the Oregon Fish Commission Laboratory, Clackamas, Oreg.; warm-water experiments were done in the Columbia River near Bonneville Dam. Frozen fish were thawed in air for 24 hours before submersion for testing; they were from the same lots as those that were later tagged and released to estimate the population of dead salmon. Fresh fish were purchased from commercial fishermen and were submerged within a few hours after death. The time required to float was calculated from the time the fish was placed in the water until some part was visible at the water surface.

In the cold-water temperature range (7.2°–11.1° C.) frozen salmon took 2.3 days longer to float than fresh salmon (appendix table 1), whereas in the warm range (12.8°–17.2° C.) the difference was reduced to 1.7 days (appendix table 2). We tested the significance of these differences by using Wilcoxon rank sum tests for comparison of group means. This nonparametric test does not require that any assumption be made concerning the distributions of floating times in the populations from which our samples are drawn. When fresh and frozen carcasses were compared under cold-water conditions (appendix table 1), the null hypothesis that there is no difference in floating times between the two types of carcasses was accepted at the 90-percent level of significance. A similar result was obtained for warm-water conditions (appendix table 2). Appendix figure 1 shows the similarity of floating characteristics of fresh and frozen carcasses, especially at relatively warm water temperatures of over 10° C. The temperature of the Columbia River was 14.4° C. during the experiment to estimate the population of dead salmon.

Next we compared floating times of carcasses in warm and cold water, again using the Wilcoxon rank sum test. Because no differences had been found between fresh and frozen carcasses, both types of carcasses were included in the comparison between water temperatures. We rejected (at the 99-percent significance level) the null hypothesis

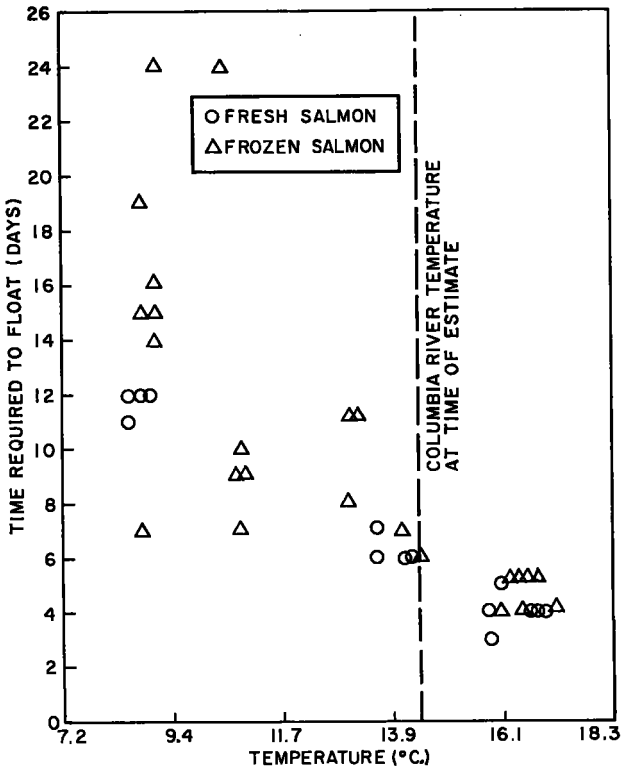
APPENDIX TABLE 1.—*Days required for fresh and frozen chinook salmon to float in cold water (7.2°–11.1° C.)*

Fresh chinook salmon			Frozen chinook salmon		
Water temperature	Days required to float	Average days required to float	Water temperature	Days required to float	Average days required to float
° C.	*Number*	*Number*	*° C.*	*Number*	*Number*
7.2–10.0	11	11.8	7.2–10.6	15	14.1
7.2–10.0	12		7.2–10.6	7	
8.3–10.6	12		7.2–10.6	19	
8.3–10.6	12		7.2–11.1	24	
			8.3–10.0	16	
			8.3–10.0	14	
			8.3–10.0	15	
			10.0–11.1	24	
			10.6–11.1	10	
			10.6–11.1	7	
			10.6–11.1	9	
			10.6–11.1	9	

APPENDIX TABLE 2.—*Days required for fresh and frozen chinook salmon to float in warm water (12.8°–17.2° C.)*

Fresh chinook salmon			Frozen chinook salmon		
Water temperature	Days required to float	Average days required to float	Water temperature	Days required to float	Average days required to float
° C.	*Number*	*Number*	*° C.*	*Number*	*Number*
13.3–13.9	7	4.6	12.8–13.3	11	6.3
13.3–13.9	6		12.8–13.3	11	
13.3–14.4	[1] <6		12.8–13.3	8	
13.3–14.4	[1] <6		13.3–14.4	[1] <6	
15.6–16.1	3		13.3–14.4	7	
15.6–16.1	4		15.6–16.7	4	
15.6–16.7	5		15.6–16.7	5	
16.7–17.2	4		15.6–16.7	5	
16.7–17.2	4		15.6–16.7	5	
16.7–17.2	4		16.7–17.2	5	
			16.7–17.2	4	
			16.7–17.2	4	

[1] These observations omitted from calculations of means and statistical comparisons of floating times.



APPENDIX FIGURE 1.—Days required for fresh and frozen chinook salmon to float at water temperatures of 7.2° to 17.2° C.

that floating time is unaffected by water temperature.

To determine whether massive tissue damage such as ruptured body cavities might affect the time required to float, we made another experiment with 15 frozen carcasses. Slits of 2.5 to 7.5 cm. were made in the body wall of eight carcasses, and full-length slits (from vent to isthmus) were made in seven.

Three fish, two with full length slits and one with a 7.5-cm. slit, took only 4 or 5 days to float at temperatures of 15.6° to 18.3° C. Of the remaining 12 fish, tested at water temperatures of 9.4° to 11.1° C., all but two floated—one of these had a 2.5-cm. slit and the other had a full-length slit. Except for the two that did not float, the time required for slit fish to float was about the same as for intact fish: in the warm-water range, slit fish required an average of 4.3 days to float compared with 4.6 days for intact fish; in the cold-water range, slit fish required an average of 12.8 days to float compared with 11.8 days for intact fish.

All the tagged experimental carcasses used for the population estimates were intact. Some of the natural population of killed fish had massive wounds, and part of these could not float and be recovered as floaters. Therefore, in the main body of this report we have referred to such fish as being unrecoverable, and in our basic model we allow for the possibility that a fraction of the fish that die are rendered unrecoverable.

Pertinent results of the flotation experiment are summarized as follows:

1. All intact dead chinook salmon, fresh or frozen, floated.
2. The relation between water temperature and time required to float was inverse, i.e., the colder the water the greater the time required for the carcass to float.
3. No statistically significant or practical differences were found between floating times of fresh and frozen fish over the range of temperatures tested.
4. A slit or puncture of the abdominal wall usually did not greatly affect the floating qualities of the fish.
5. Fresh and frozen chinook salmon carcasses have similar floating properties; therefore, frozen carcasses can be used to simulate fresh carcasses.

Disappearance of Floaters from Recovery Area

We conducted another experiment to estimate the rapidity of disappearance of floaters from the surface of the Columbia River within the recovery area and to trace their dispersion from the point of first appearance. From April 4 to July 22, 1955, all floaters in reasonably good condition were tagged with Petersen disks and released where they were found (appendix table 3). Of 289 chinook salmon floaters tagged, 11 percent were recovered; 26 were recovered again after the first release, and five after a second release. The single recovery from the 17 chinook salmon released above the dam at station 8 (The Dalles) was by a fisherman about 4.8 km. downstream from the release point. Nineteen percent of the 11 steelhead floaters were recovered. The greatest distance traveled by any tagged floater before recovery below the dam was 74 km.

APPENDIX TABLE 3.—*Number of floaters tagged at search stations near Bonneville Dam and percentage recovered, April 4 to 22, 1955*

Tagging location	Chinook salmon		Sockeye salmon		Steelhead trout	
	Tagged	Recovered	Tagged	Recovered	Tagged	Recovered
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
The Dalles	17	1	4	0	0	0
Bonneville [1]	32	0	5	0	2	0
Cape Horn	75	6	21	0	0	0
Reed Island	92	13	3	1	3	0
Ellsworth	17	4	15	1	2	0
Willamette	63	4	13	1	4	1
St. Helens	3	3	0	0	0	1
Total	[2] 299	[3] 31	61	3	11	2
Percent recovered		11		5		19

[1] McGowan and Moffett Creek stations combined.
[2] Including 26 released twice and five released a third time.
[3] Including five second recoveries.

Tags from eight of the 272 chinook and three of the 57 sockeye salmon released downstream from the dam were returned by fishermen; the rest were recovered at search stations.

Forty-four chinook and 12 sockeye salmon were released at stations 1 (St. Helens) and 2 (Willamette) when there was no search effort farther downriver. These fish, therefore, had no chance for recovery at search stations. In both years, carcasses released at stations farther downstream had less chance of recovery than those released farther upriver because the number of search stations was smaller downstream from the dam.

Only five of the 22 chinook salmon floaters recovered at search stations in 1955 traveled more than 16 km., and all but one were found the same day they were released. Thus, the small number of second recoveries of tagged floaters was indicative of their rapid disappearance.

Tagging and recovery of floaters also provided useful information on their rate of travel: during our experiment in July 1955, when river flow was high, the rate below Bonneville Dam was from 3.4 to 5.1 km.p.h. (average 4.2 km.p.h.).

Thus, during the period of recovery of tagged floaters for the mortality estimate, a floater required a maximum of only 16 hours to pass through the entire search area between the dam and the mouth of the Willamette River, a distance of 70 km.

From these facts, the following conclusions may be drawn regarding disappearance and rate of travel of floaters:

1. Floaters appearing at the surface near Bonneville Dam would pass through the 70-km. search area between the dam and the mouth of the Willamette River in less than 16 hours, provided they remained in the current.

2. Floaters would pass through the entire search area during the night between successive days of sampling, eliminating any possibility of being observed.

3. Floaters originating near the dam would reach the mouth of the Columbia River in 3 or 4 days.

FOOD OF YOUNG ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, IN RELATION TO METAMORPHOSIS

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ABSTRACT

To rear this species in captivity required knowledge of the kinds of organisms it ate. Larvae ate zooplankton (copepods), but prejuveniles and juveniles fed chiefly on phytoplankton. There were similarities as well as differences between the alimentary tract contents of the fish and the composition of the plankton community. Changes in food habits during metamorphosis were accompanied by gross morphological changes in the alimentary tract and related structures. Laboratory studies of larvae disclosed that their failure to feed at low light intensities, their digestion rate, and their defecatory response to capture and preservation probably contributed to the high incidence of empty alimentary tracts in field collections.

Laboratory research is needed to determine how specific environmental factors affect the distribution, behavior, and survival of young Atlantic menhaden (*Brevoortia tyrannus*) after their entry as larvae into estuarine nurseries from oceanic spawning grounds (June and Chamberlin, 1959). Before these young fish can be successfully maintained in the laboratory, it is necessary to know their diet requirements.

Previous investigators established that young Atlantic menhaden feed on plankton. Peck (1894) observed that stomach contents of juveniles (60 and 100 mm. long) collected near Woods Hole, Mass., closely agreed with the plankton in the surface waters. He also described the specialized gill rakers that this fish uses to strain minute organisms from the water. Using radioisotope techniques, Chipman (1959) determined that larvae were unable to filter phytoplankton, but fed on larval brine shrimp and on copepods. Juveniles (averaging 188 mm. long), on the other hand, could filter phytoplankton cells (*Nannochloris*) as small as 2 μ. Richards (1963a, 1963b) found crustaceans (chiefly *Balanus* larvae, *Neomysis*, and the copepods *Centropages*, *Paracalanus*, *Acartia*, and *Temora*) to be the principal food of 29 specimens (16–120 mm. long) from Long Island Sound, N.Y. She reported no differences in stomach contents of fish of different sizes.

None of the earlier investigators clearly identified the changes in composition of diet associated with the transformation of Atlantic menhaden larvae into juveniles.[3] Because our principal aim was to establish techniques for rearing laboratory stocks of these young fish through metamorphosis for experimental purposes, we needed to know their food requirements at the different developmental stages and the suitability of substitute foods. Moreover, in connection with studies of the estuarine ecology of young menhaden in progress in Indian River, Del. (June, 1957), it was essential to know their natural foods so as to assess the relevant components of the plankton. Finally, changes in morphology of the digestive system that enable juveniles to feed on smaller

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[3] We follow the definitions of Mansueti and Hardy (1967). Larva: The stage of development between hatching and attainment of the adult fin-ray complements; our specimens ranged from 13 to about 30 mm. fork length. Prejuvenile: The intermediate stage between larval and juvenile form; these ranged from about 30 to 40 mm. fork length. Juvenile: Young fish after attainment of full adult counts and before sexual maturation; the stage begins when the body form closely approximates that of the adult and in our specimens occurred at about 40 mm. fork length.

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plankters than larvae had not been previously described. Most of our research on these subjects was done at the former Field Station of the BCF (Bureau of Commercial Fisheries) at Millville, Del., in 1960 and 1961.

STUDIES OF ALIMENTARY TRACT CONTENTS AND PLANKTON COMPOSITION

We determined the natural foods of young Atlantic menhaden by examining the alimentary tract contents of wild specimens. Analysis of concomitant plankton samples enabled us to compare the organisms available and those actually ingested.

MATERIALS AND METHODS

Alimentary tracts of 738 young menhaden were examined for food. Of this number, 592 came from larvae chosen at random from catches made with 1-m.-diameter nylon plankton nets (mesh aperture 0.90 mm.) in the mouth of Indian River, Del., between November 1960 and May 1961 (table 1). The rest came from larvae, prejuveniles, and juveniles captured by haul seines within this estuary from April to June 1961 (table 2).

Preservation techniques varied with the size of the fish and character of the alimentary tract contents. Larvae were preserved intact in 5 percent Formalin [4] buffered with borax. The alimentary tract from most prejuveniles and juveniles was removed, slit longitudinally, and preserved in a chrom-osmic mixture (Gray, 1954); some tract contents were only chilled prior to examination.

The fraction and portion of the tract contents examined also varied with the developmental stage of the fish. The alimentary tract of larvae was opened, the percentage fullness estimated, and the location of contents within the tract noted. Organisms were removed, identified, counted, and measured; and the relative volume of each item was estimated. With prejuveniles and juveniles, only the contents of the esophagus and anterior stomach were examined, because we could recognize few organisms

[4] The use of trade names in this publication does not imply endorsement of commercial products.

TABLE 1.—*Samples of Atlantic menhaden larvae for food studies collected in plankton nets at Indian River Inlet, Del., November 1960 to May 1961*

Date	Time of collection	Larvae examined	Alimentary tracts containing food		Mean number of organisms per tract containing food	Fork length of larvae with food		Sky condition at time of collection
						Range	Mean	
		Number	*Number*	*Percent*	*Number*	*Mm.*	*Mm.*	
1960								
November 7	0855–0955	30	18	60	4	19–25	22.3	Clear
29	0325–0425	11	0	0	0			Obscured by dense fog
December 2	1810–1910	11	1	9	3	32		Clear (dark); followed by rising full moon
6	0840–0940	2	2	100	5	26–28	27.0	Obscured by clouds
8	2155–2255	5	1	20	2	30		Partly cloudy
12	1325–1505	56	46	82	2	24–32	28.3	Do.
16	1725–1825	40	18	45	2	23–30	27.3	Clear (dark)
19	1910–2010	54	32	59	5	24–29	26.8	Do.
20	0155–0255	53	9	17	2	24–30	26.6	Clear
20	0730–0840	14	0	0	0			Partly cloudy
22	2140–2240	9	7	78	3	26–34	28.6	Clear; ¼ moon
28	0235–0335	50	14	28	3	23–29	27.4	Clear; ¾ moon
28	0910–1010	3	2	67	2	26–28	27.0	Partly cloudy
28	1517–1617	21	13	62	5	23–29	26.0	Do.
28	2130–2230	18	6	33	3	23–27	25.7	Do.
30	1730–1830	55	35	64	3	23–28	26.2	Clear; full moon
1961								
January 2	1900–2000	46	22	48	3	22–28	26.0	Do.
3	0040–0140	5	1	20	2	21		Do.
3	0655–0755	48	7	14	1	23–28	25.7	Clear
16	1755–1855	5	2	40	1	27–29	28.0	Clear (dark)
16–17	2355–0055	6	1	17	1	25		Clear
17	0630–0730	7	2	28	2	24	24.0	Do.
May 9	0235–0335	43	4	9	1	28–30	29.0	Do.
Total		592	243		3	19–34		

TABLE 2.—*Samples of Atlantic menhaden larvae, prejuveniles, and juveniles for food studies collected in haul seines within the Indian River estuary, Del., April to June 1961*

Date	Number of alimentary tracts examined	Alimentary tracts containing food	Fork length of fish with food	
			Range	Mean
	Number		*Mm.*	*Mm.*
April 27	20	7	30–37	33.7
June 5	45	44	28–46	35.9
20	10	10	65–94	81.0
23	27	27	33–75	57.7
23	10	10	75–90	83.8
30	26	15	68–75	71.9
30	8	4	68–78	73.5
Total	146	117	28–94	

in the pyloric stomach (gizzard) and intestine. Identifiable contents were treated in the same manner as the contents of the alimentary tracts of the larvae. Diatoms were cleared by the Van Der Werff (1955) method and mounted in hyrax before examination.

Concomitant plankton samples were usually taken for each fish collection. Zooplankton was collected with a high-speed sampler described by Miller (1961) and monofilament nylon net (mesh aperture 0.24 mm.). Most samples were preserved in 5 percent buffered Formalin. Phytoplankton was collected in a 140-ml. water sampler and preserved with the chrom-osmic mixture used for contents of alimentary tracts. Some zooplankton and phytoplankton samples were only chilled prior to examination. Organisms in aliquots of preserved and fresh plankton samples were identified, counted, and measured. Diatoms, when present, were cleared (Van Der Werff, 1955) and mounted in hyrax.

FOOD OF MENHADEN AND RELATIONS TO ESTUARINE PLANKTON

We took samples at the inlet and within the estuary.

Samples at the Inlet

The contents of the alimentary tracts of larvae consisted of zooplankton. Of 592 tracts examined, 349 (59 percent) were empty. Of the 243 that contained food, 52 percent were less than one-quarter full, 28 percent were about half full, and 20 percent were over half full. The contents were 99 percent copepods, of which *Centropages* was the most common of those identified (table 3). The number of food organisms averaged 3 per alimentary tract, but varied between 1 and 12. Composition of tract contents showed no apparent changes during the sampling period.

The size of copepods ingested varied widely (0.65–2.00 by 0.16–0.65 mm.) but generally increased with fish length (fig. 1). *Pseudodiaptomus* was the only copepod found in larvae under 23 mm. long. *Centropages* occurred in larvae 23 mm. and longer, whereas *Acartia* and *Temora* were found in specimens from 24 to 30 mm. long.

TABLE 3.—*Alimentary tract contents of 243 Atlantic menhaden larvae collected at Indian River Inlet, Del., November 1960 to May 1961*

Food item	Alimentary tracts containing organisms	Mean number of organisms per tract	Total tract contents	Size of organisms			
				Range		Mean	
				Length	Width	Length	Width
	Number	*Number*	*Percent*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Zooplankton							
Copepoda							
Centropages	72	<1	18.7	0.85–2.00	0.30–0.65	1.29	0.41
Acartia	26	<1	9.5	0.85–1.58	.24–.60	1.28	.38
Pseudodiaptomus	15	<1	6.7	0.65–1.20	.16–.35	1.07	.31
Temora	6	<1	1.6	1.20–1.48	.48–.52	1.34	.50
Tortanus	2	<1	0.2	1.70	.54	1.70	.54
Unidentified copepods	189	2	62.3				
Total copepods	238	3	99.0				
Pelecypoda	7	<1	0.8	0.37–0.46	.30–.37	0.40	.34
Phytoplankton							
Centrales							
Coscinodiscus	1	<1	0.1	0.22			
Unidentified organic material	2						

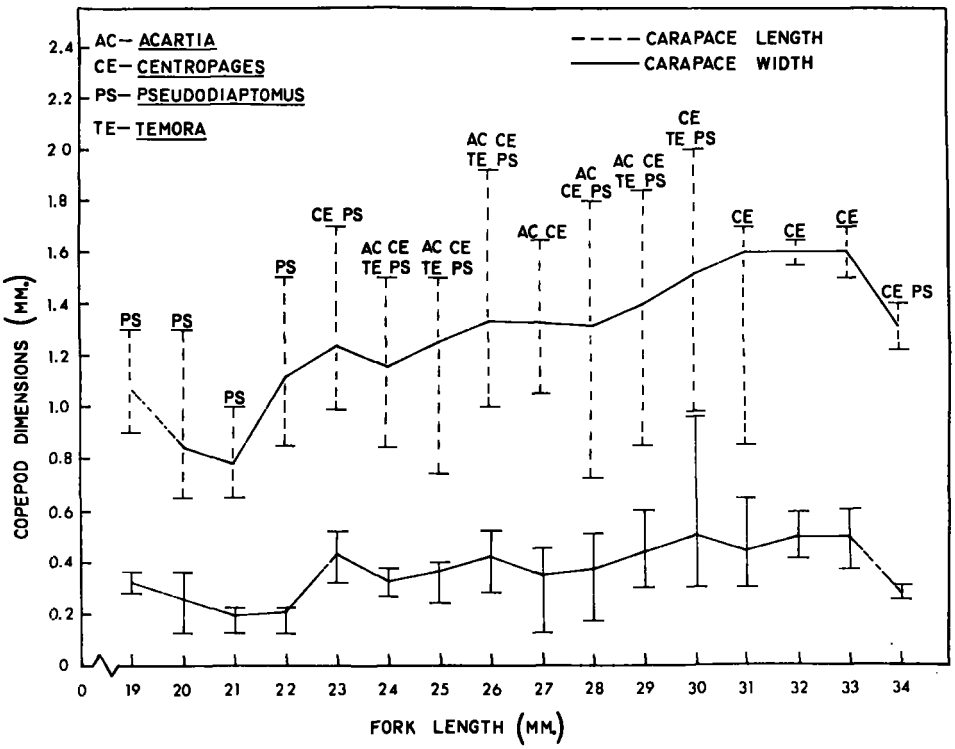

FIGURE 1.—Size of copepods ingested in relation to fork length of Atlantic menhaden larvae. Range of copepod dimensions shown by vertical lines; mean length and width shown by trend lines.

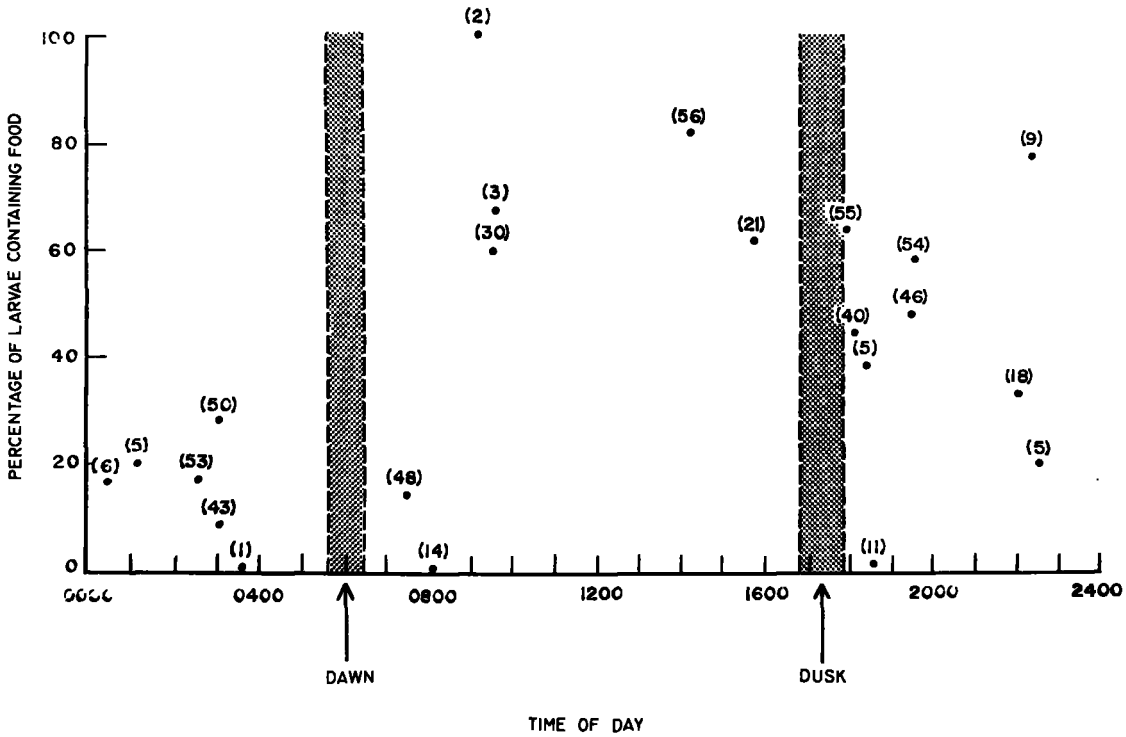

FIGURE 2.—Scatter diagram showing the relation between the number of alimentary tracts of Atlantic menhaden larvae containing food and time of collection. Number of larvae examined shown above each dot.

Percentages of larvae with food organisms in the alimentary tracts were generally higher in daylight and evening (fig. 2). Feeding activity tended to be higher on moonlit nights than on dark nights (50 percent of the larvae caught on moonlit nights contained food compared with 31 percent on dark nights).

The composition of the net plankton and the alimentary tract contents of larvae showed similarities and differences. For example, copepods accounted for 98 percent of the net zooplankton and 99 percent of the tract contents (table 4). Four genera, *Centropages, Acartia, Pseudodiaptomus,* and *Temora,* were common to both the net zooplankton and the alimentary tract contents, but their order of rank differed. With the exception of the single sample collected in May, in which the genus *Temora* predominated, *Acartia* consistently was the most abundant organism in the net zooplankton. Pelecypods were rare in both the net samples and the alimentary tracts.

Centrate diatoms dominated the phytoplankton numerically in 10 samples taken at random throughout the sampling period (table 5). Of all larval alimentary tracts examined, only one contained a single phytoplankter, *Coscinodiscus.*

Samples Within the Estuary

The contents of the alimentary tracts of larvae and smaller prejuveniles consisted of zooplankton, but changed to phytoplankton and unidentifiable material in larger prejuveniles and juveniles. Only 29 (20 percent) of the tracts examined were empty. As was found in the inlet collections, the tract contents of larvae consisted exclusively of copepods (chiefly *Acartia*). The contents of progressively larger prejuveniles gradually shifted from copepods to a mixture of greenish brown amorphous material, diatoms, and flagellates (fig. 3), and at least 80 percent (by volume) of the tract contents of juveniles consisted of these latter items. Diatom genera identified, in order of their frequency of occurrence, were *Pleurosigma, Navicula, Nitzschia, Cyclotella, Melosira, Amphora, Gyrosigma,* and *Surirella.* Flagellates identified included *Peridinium, Gymnodinium,* and *Polykrikos.*

The composition of the plankton resembled the contents of the alimentary tracts examined for the size range of fish sampled. Copepods, chiefly *Acartia,* accounted for nearly 100 percent (by volume) of the net zooplankton after

TABLE 4.—*Composition of fauna in 23 tow-net samples taken concomitantly with collections of Atlantic menhaden larvae at Indian River Inlet, Del., November 1960 to May 1961*

Organisms	Samples containing organisms	Mean number of organisms per cubic meter	Percentage of total organisms	Size of organisms			
				Range		Mean	
				Length	Width	Length	Width
	Number	*Number*	*Percent*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Chaetognatha	19	3	<0.1	4.50–14.60	0.22–0.75	9.41	0.46
Copepoda							
Acartia	23	2,228	55.6	0.89– 1.55	0.26–0.37	1.20	.33
Temora	10	2,194	23.8	1.40– 1.76	0.40–0.59	1.49	.50
Centropages	23	457	11.4	0.88– 1.92	0.30–0.58	1.51	.43
Pseudodiaptomus	20	312	6.8	1.09– 1.85	0.28–0.68	1.36	.40
Tortanus	4	3	<0.1	1.68– 1.96	0.44–0.65	1.85	.51
Labidocera	4	23	0.1	2.07– 2.75	0.45–0.74	2.43	.64
Rhincalanus	2	1	<0.1	3.03	0.52	----	----
Eucalanus	1	<1	<0.1	2.25	0.60	----	----
Unidentified nauplii	2	4	<0.1	0.81	0.30–0.37	----	.33
Ostracoda	3	1	<0.1	0.63– 1.18	0.37–0.48	0.85	.43
Malacostraca							
Mysidacea	21	92	2.1	2.55– 6.75	0.30–1.50	5.87	.63
Isopoda	7	1	<0.1	1.80–21.00	0.68–7.00	----	----
Decapoda	13	3	<0.1	1.32–52.00	0.30–1.80	----	----
Amphipoda	9	3	<0.1	1.32– 5.70	0.31–1.50	3.55	.63
Pelecypoda	8	6	<0.1	0.36– 1.20	0.20–0.60	0.65	.38
Miscellaneous	13	5	<0.1	0.36– 5.25	0.35–0.90	----	----

TABLE 5.—*Composition of phytoplankton in 10 water samples taken concomitantly with collections of Atlantic menhaden larvae at Indian River Inlet, Del., November 1960 to May 1961*

Organisms	Samples containing organisms	Estimated mean number of organisms per liter	Percentage of total
	Number	*Number*	*Percent*
Pennales			
Nitzschia	2	372	0.4
Pleurosigma	6	559	1.9
Gyrosigma	1	293	0.2
Navicula	3	398	0.7
Diploneis	2	186	0.2
Cocconeis	2	132	0.2
Achnanthes	3	657	1.1
Thalassiotrix	8	1,310	6.1
Asterionella	7	783	3.2
Centrales			
Bellerochea	1	483	0.3
Biddulphia	1	500	0.3
Corethron	1	426	0.2
Rhizosolenia	1	2,909	1.7
Actinoptychus	6	775	2.7
Coscinodiscus	9	3,403	17.8
Thalassiosira	7	2,560	10.4
Cyclotella	5	942	2.7
Skeletonema	8	8,689	40.3
Melosira	7	672	2.7
Diatoms other than above genera	6	1,525	5.3
Peridiniales			
Peridinium	2	1,525	0.3
Prorocentrales			
Gyrodinium	2	459	0.3
Prorocentrum	1	237	0.1
Exuviella	1	237	0.1
Unidentified flagellates	2	604	0.7

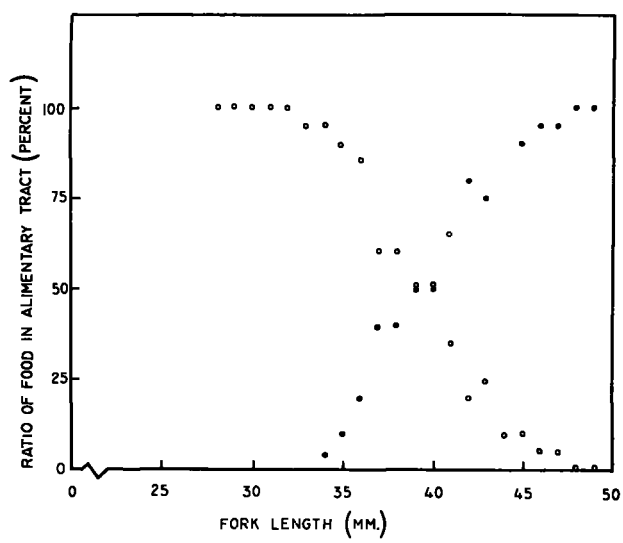

FIGURE 8.—Volume ratio of copepods and amorphous food material (chiefly phytoplankton) in alimentary tracts of young Atlantic menhaden in relation to fork length. Open circles represent copepods and solid circles amorphous material.

removal of the ctenophores, *Pleurobrachia* and *Mnemiopsis*, from the samples. Phytoplankton consisted of naked and thecate flagellates (mainly *Polykrikos*, *Peridinium*, and *Gymnodinium*), and diatoms (chiefly *Pleurosigma* and *Coscinodiscus*). Similarities between the color and form of the greenish brown materials found in the alimentary tracts of the fish and the fragile flagellates in water samples suggested to us that the amorphous residue was the remnants of these organisms.

Our studies of the natural food of young Atlantic menhaden confirmed that they are plankton feeders. As larvae they feed only on zooplankton but during metamorphosis they increase their capability to retain smaller phytoplankters. During its early life stages, this fish directly utilizes the abundant standing crops of both phytoplankton and zooplankton in estuaries. No other marine fish now occupies this ecological role in Atlantic Coast estuaries.

The occurrence of young Atlantic menhaden within the Indian River estuary appeared to be associated with the seasonal cycle of plankton production. Our highest catches of larvae at the inlet were made in December and January (69 and 66 larvae per tow, respectively, as compared with 0 to 9 per tow in other months) and coincided with the maximum monthly catches of each of the four dominant copepods represented in our net samples (*Centropages*, *Acartia*, *Pseudodiaptomus*, and *Temora*). Metamorphosis of menhaden larvae began in April 1961 and followed a phytoplankton flowering in this estuary in late March. Jeffries (1964) also found that the occurrence of Atlantic menhaden larvae in Raritan Bay coincided with the seasonal peak of *Acartia tonsa* in that locality. Apparently, seasonally abundant estuarine populations of copepods (Deevey 1956, 1960) provide an available food supply for the carnivorous larvae when they enter the estuary, and high standing crops of phytoplankton (Riley, 1967) are available during and following the metamorphosis of larvae into juveniles within the estuary.

STUDIES OF MORPHOLOGICAL CHANGES DURING METAMORPHOSIS OF YOUNG MENHADEN

As Atlantic menhaden larvae transform into juveniles, they acquire scales, fin-ray complements, and the deep body form characteristic of adults (Mansueti and Hardy, 1967). The shift from a carnivorous to an omnivorous diet during metamorphosis suggests that changes also take place in structures directly concerned with feeding and digestion.

MATERIALS AND METHODS

Changes in the morphology of structures associated with feeding and digestion were described from counts or measurements as a function of fish length. The counts or measurements were made on 196 specimens, 19 to 75 mm. long, from the samples of fish used for the food studies and included the following:

Dentary teeth: Total along margin of left dentary.

Fork length: Distance (1.0 mm.) from tip of mouth to end of median rays in caudal fin.

Gape height: Distance (0.1 mm.) between inner margins of premaxillary and dentary symphyses with jaws opened to a 65° angle.

Gape width: Distance (0.1 mm.) between inner margins of jaw angles opened to a 65° angle.

Gill rakers: Total, including rudiments, along first left gill arch.

Length of the anterior alimentary tract: Distance (0.1 mm.), with tract extended, between posterior margin of pharynx and the pylorus.

Length of the posterior alimentary tract: Distance (0.1 mm.), with tract extended, between the pylorus and anus.

Maxillary teeth: Total along margin of left maxillary.

Pyloric caeca: Total evaginations at juncture of anterior and posterior alimentary tracts.

DEVELOPMENT OF THE DIGESTIVE SYSTEM IN RELATION TO DIET

We studied morphological changes in the mouth, teeth, gill rakers, alimentary tract, and pyloric caeca during metamorphosis and related these changes to the diet.

Mouth

The terminal mouth of the Atlantic menhaden larva has an elliptical opening and is relatively large through later stages of development (fig. 4). A median notch is present on the upper jaw of larvae over 19 mm. long, and the lower jaw is included in the upper one. The mouth opening in 19-mm. larvae is about 1 mm.^{2}; it increases to a maximum of about 7 mm.^{2} in prejuveniles and reaches about 20 mm.^{2} in 75-mm. juveniles. Because gape height and width increase linearly with length of the fish (fig. 5), the maximum dimension

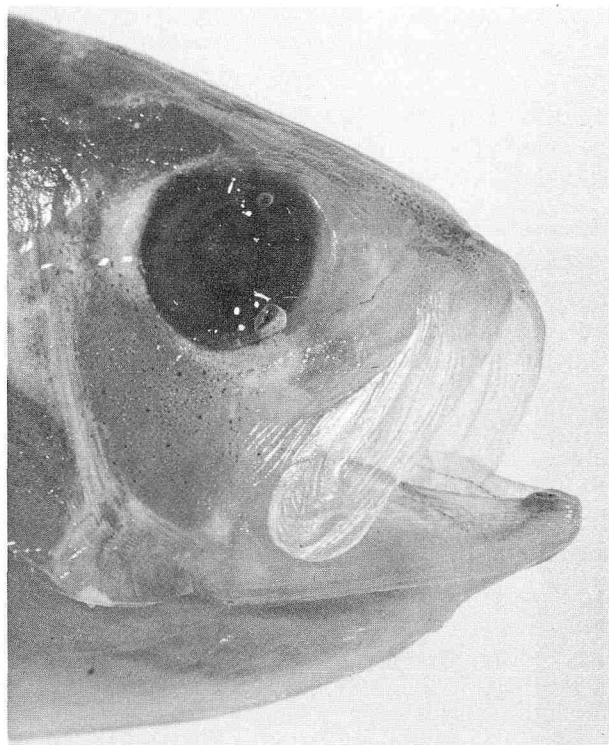

FIGURE 4.—Lateral view of the head of a 75-mm. (fork length) juvenile Atlantic menhaden showing the gape and the median notch on the upper jaw.

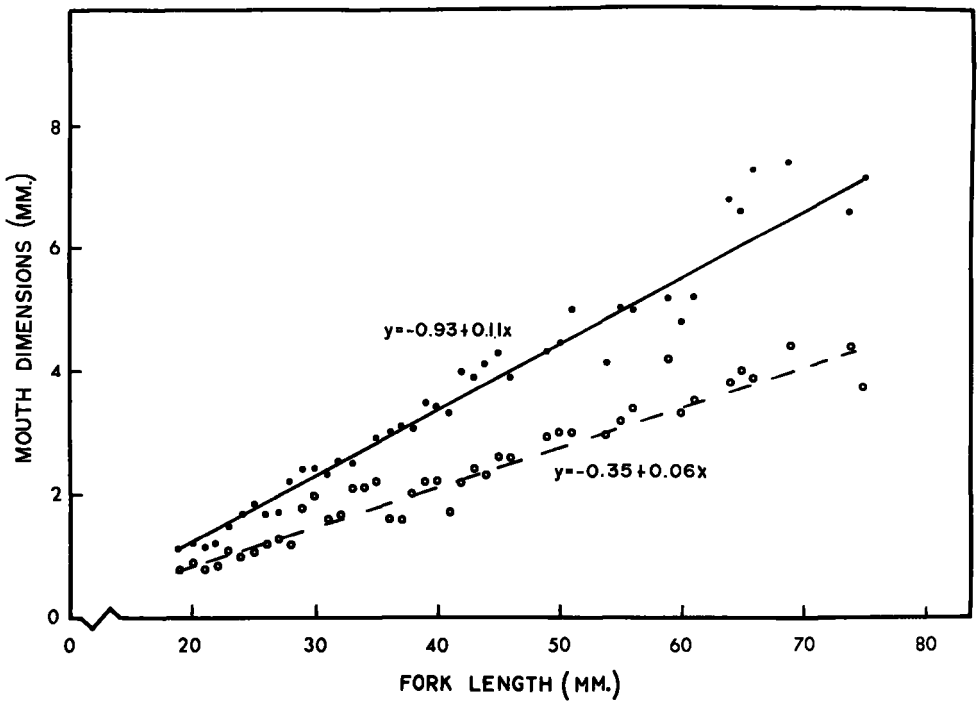

FIGURE 5.—Regression of gape height (solid circles) and gape width (open circles) on fork length of young Atlantic menhaden. Circles represent means of a group of measurements; regression lines were computed from measurements of 124 fish.

of organisms that the fish might ingest would increase from about 0.6 mm. in a 19-mm. larva to about 7.0 mm. in a 75-mm. juvenile.

Teeth

Teeth are prominent in larvae but largely absent in juveniles. Maxillary teeth of larvae are in a single row on the anterior margin of the bone (table 6). Each tooth is 30 to 40 μ long, irregularly shaped, but usually pointed, and has a wide base (fig. 6). These teeth increase in number in prejuveniles, become partially embedded in tissue, and form two or three overlapping rows on the flank of the maxillary. After metamorphosis, maxillary teeth apparently are nonfunctional and eventually disappear.

Dentary teeth occur as slightly recurved conical projections, each 25 to 30 μ long, on the medial anterior edge of the bone (fig. 7). These teeth are conspicuous in larvae and prejuveniles but disappear in juveniles (table 6).

Specialization of the mouth structures in relation to actual food consumed by young Atlantic menhaden is indicated. The large terminal mouth and recurved marginal teeth in larvae are adapted for the capture and retention of zooplankters. Dentition would seem to be

TABLE 6.—*Tooth counts of young Atlantic menhaden*

Fork length	Teeth on left side	
	Maxillary	Dentary
Mm.	*Number*[1]	*Number*[1]
19	12	4
20	13	4
21	16	4
22	16	4
23	20	4
24	20	4
25	16	4
26	18	4
27	17	4
28	22	4
29	21	4
30	24	4
31	25	4
32	25	4
33	27	4
34	25	4
35	24	4
36	26	3
37	28	2
38	24	2
39	23	2
40	25	1

[1] Average of counts on two specimens.

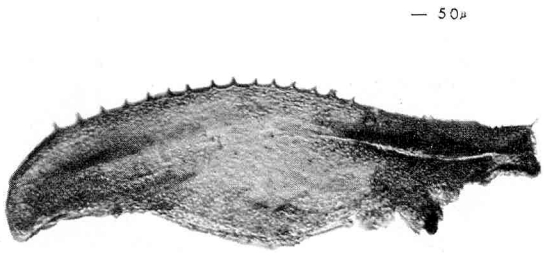

FIGURE 6.—Exterior view of left maxillary bone of a 22-mm. (fork length) Atlantic menhaden larva showing the single row of teeth; posterior end on left.

FIGURE 7.—Top interior view of dentary bones of a 22-mm. (fork length) Atlantic menhaden larva showing the single row of teeth (1 division=50 μ).

superfluous for ingesting the smaller organisms that compose the phytoplankton; dentition becomes nonfunctional after metamorphosis.

Gill Rakers and Accessory Structures

During metamorphosis the gill rakers increase in length, number, and complexity. In larvae under 25 mm. long the lower limb (consisting of the hypobranchial and the ceratobranchial segments) and the upper limb (epibranchial segment) are slightly curved. Rakers initially form as rounded protuberances at the angle between the upper and lower limbs (fig. 8); those of the lower limb appear first. Two

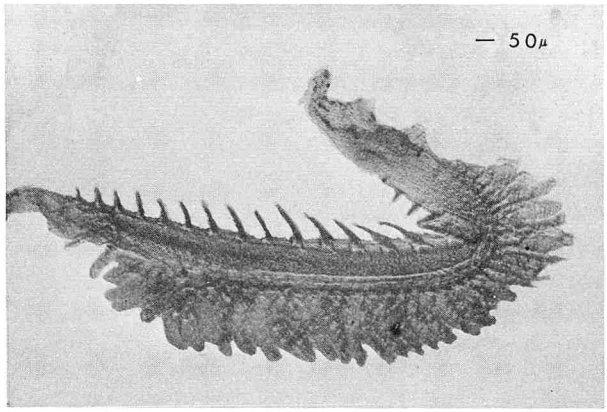

FIGURE 8.—First left gill arch of a 20-mm. (fork length) Atlantic menhaden larva showing the rudimentary rakers on the upper and lower limbs.

rows of barbs appear along the longitudinal axis of individual rakers. As fish increase in length, the rakers become distinctly elongate. Barbs increase in number, become slightly curved, and ultimately develop a serrate tip (fig. 9). The hypobranchial segment of the first gill arch becomes more curved anteriorly; rakers continue to form at the anterior ends of the epibranchial and hypobranchial segments, while those near the angle on the upper

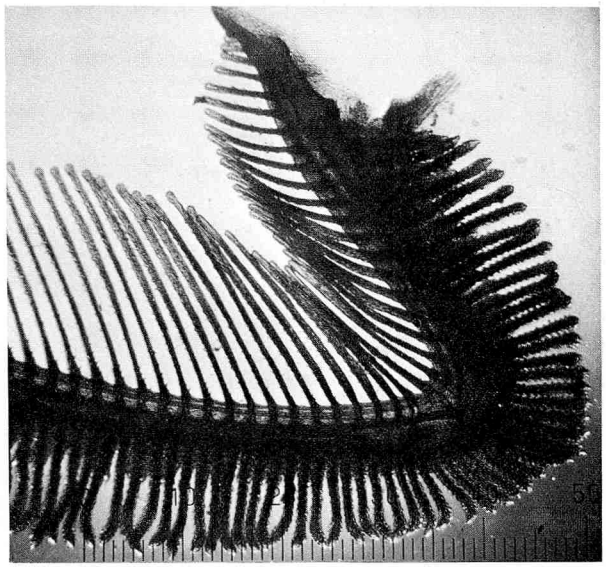

FIGURE 9.—Photomicrograph showing the barbs on the rakers of the first left gill arch of a 32-mm. (fork length) Atlantic menhaden prejuvenile (1 division = 50 μ).

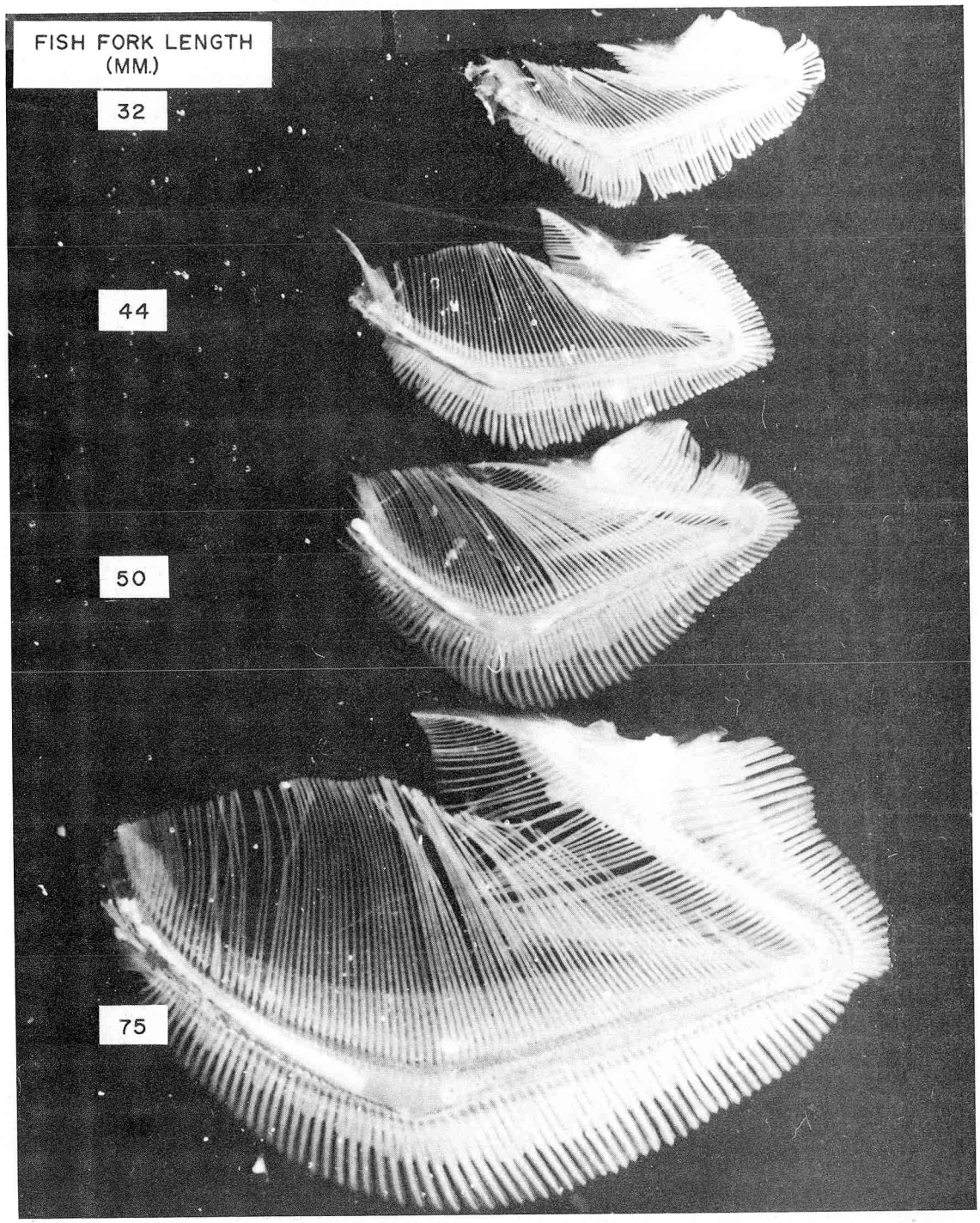

FIGURE 10.—Photomicrograph showing the structure of the gill rakers and the increase in relative size of the first left gill arch of young Atlantic menhaden.

limb extend downward and lie over those on the upper part of the lower limb (fig. 10). The number of rakers on the first left gill arch is variable and a nonlinear function of length

over the range examined (table 7). The number of rakers progressively decreases on the second, third, fourth, and fifth arches.

TABLE 7.—*Gill-raker counts of young Atlantic menhaden*

Fork length	Specimens examined	Range of gill-raker counts: Upper limb	Lower limb	Total	Mean total count
Mm.	*Number*	*Number*	*Number*	*Number*	*Number*
20–24	14	0–10	10– 22	12– 29	20
25–29	13	7–17	17– 35	24– 52	35
30–34	10	15–26	30– 48	47– 69	60
35–39	11	24–40	44– 58	69– 87	75
40–44	12	29–40	47– 63	79–103	89
45–49	5	36–44	57– 63	93–117	103
50–54	5	42–48	64– 79	106–127	118
55–59	5	45–55	68– 78	113–133	121
60–64	5	48–61	73– 81	121–136	129
65–69	5	54–64	86– 96	145–150	149
70–74	5	59–62	93–101	152–160	155

The fold of mucous membrane, which forms a groove along the bone of the gill rakers in adult Atlantic menhaden (Peck, 1894), appears as a transparent ridge in larvae (fig. 8). In prejuveniles the ridge becomes a distinct pigmented groove with an opening at the juncture of each branch of the gill arch (fig. 10). The function of this structure is not clear, but it may aid channeling food organisms posteriorly.

Pharyngeal pockets, described in clupeids by Hyrtl (1855) and in *Brevoortia* by Monod (1961), are first evident in larvae 25 mm. long. These structures appeared as two slight swellings, one on each side of the longitudinal plane, above the pharynx and anterior to the fifth gill arch. In prejuveniles the pockets become pigmented and kidney-shaped; their size increases as the length of the fish increases. Lagler and Kraatz (1945) postulated that the pharyngeal organ in the gizzard shad, *Dorosoma cepedianum*, is accessory to the digestive tract, rather than to the respiratory system as suggested by Hyrtl (1855). The presence of fresh food organisms in these structures in Atlantic menhaden suggests that the pharyngeal pockets are part of the digestive system and may accumulate the plankton prior to swallowing.

The change from a zooplankton to a phytoplankton diet in young Atlantic menhaden is thus associated with developmental changes in the gill-raker complex. Peck (1894) described the gill rakers of adults as being ". . . so complete as to render the whole pharyngeal cavity capable of filtering large quantities of water . . ." The gill rakers of larvae, however, are rudimentary and have no obvious function. So the incorporation of phytoplankton into the diet of prejuveniles and juveniles seems to be largely a function of the straining capacity of the gill rakers.

Alimentary Tract

Like the gill arch complex, the alimentary tract undergoes remarkable changes during development. In larvae the tract is nearly a straight tube connecting the pharynx and the anus. At about one-third its length, a constriction marks the junction of the stomach and intestine. The length of the anterior tract changes relatively little as the fish grows longer, but the posterior tract (intestine) changes markedly (fig. 11). When linear relations are assumed, the regression lines in figure 11 show that the length of the alimentary tract in larvae increases by about 0.3 mm. for each 1-mm. increase in length of fish; but in prejuveniles and juveniles, the length of the tract increases about 10 mm. for each 1-mm. increase in fish length.

In prejuveniles the stomach folds on itself; a blind sac develops posteriorly, forming the tail of a Y, with the pneumatic duct leading from its tip; and the lower part of the stomach (gizzard) enlarges and develops a muscular wall. Pyloric caeca are first evident in larvae 28 mm. long. Their number is variable and reaches a maximum in juveniles (table 8). In recently metamorphosed juveniles, the intestine folds on itself and forms two or three coils, the pyloric caeca lengthen, and fat is deposited among the caeca and coils of the intestine (fig. 12).

The simple straight gut of Atlantic menhaden larvae is characteristic of early clupeid development (Harder, 1958, 1960) and generally associated with a carnivorous diet in fishes (Barrington, 1957; Nikolsky, 1963). The change in food habits during metamorphosis of young menhaden is linked with changes in the digestive tract. Development of the gizzardlike pyloric stomach probably aids in the crushing of diatoms, while development of pyloric caeca

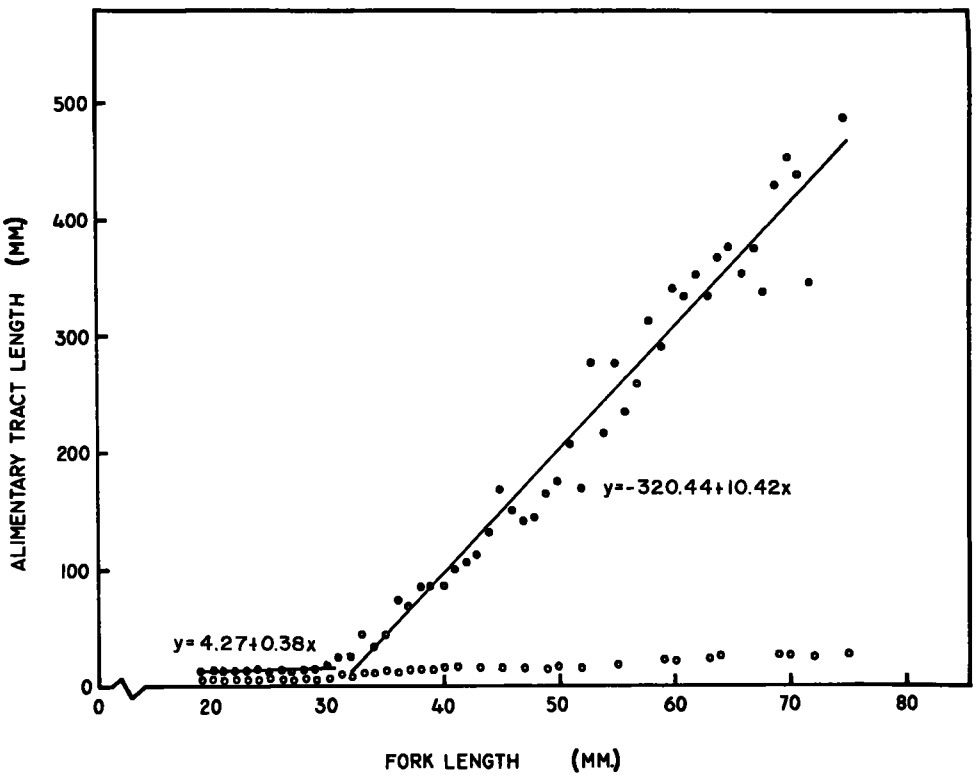

FIGURE 11.—Length of anterior alimentary tract and of total tract in relation to fork length of young Atlantic menhaden. Open circles represent group means of anterior tract measurements of 138 specimens; solid circles represent group means of the total tract length. The regression line for the 19- to 30-mm. fork length range was computed from measurements of 48 specimens and that for the 31- to 75-mm. fork length range from measurements of 90 specimens.

and the long coiled intestine increases the surface area for secretion and absorption.

LABORATORY STUDIES

We demonstrated that qualitative differences in the diet of young Atlantic menhaden were associated with changes in the gill raker-alimentary tract complex during metamorphosis, but we still did not know the quantities of food they needed for growth. The high incidence of empty or partially filled alimentary tracts in larvae captured in Indian River, Del., suggested that these quantities were small. Peck (1894) and Breder (1959) had described the feeding behavior of juveniles sufficiently for our needs, but we still did not know how larvae and prejuveniles fed nor if they could

TABLE 8.—*Pyloric caeca counts of young Atlantic menhaden*

Fork length	Pyloric caeca
Mm.	*Number*
28	241
29	277
30	446
31	312
32	299
33	303
34	254
35	372
37	288
40	355
42	368
43	299
45	440
50	357
55	351
60	323
65	437
70	411
75	436

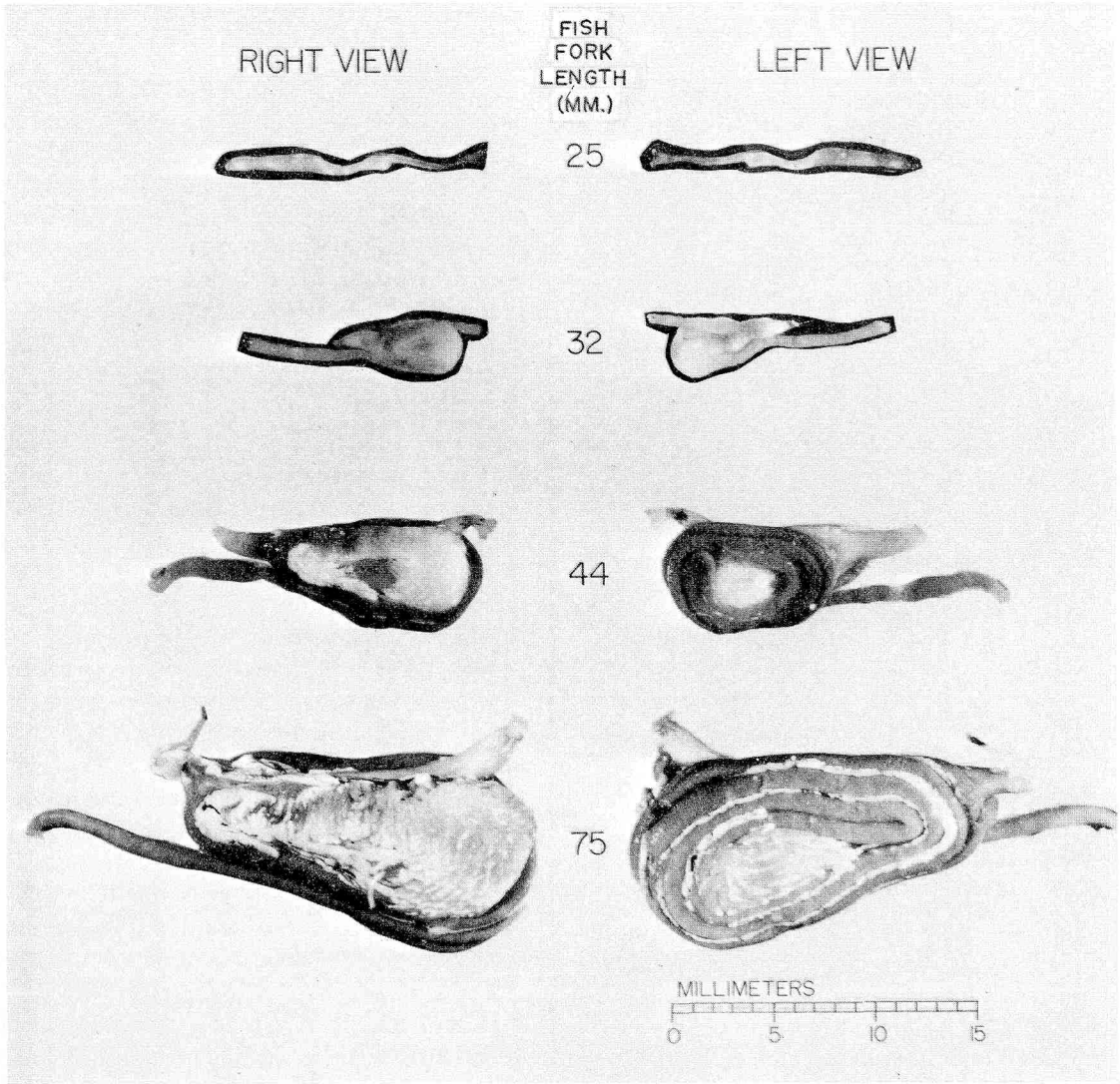

FIGURE 12.—Lateral views of the alimentary tract of young Atlantic menhaden.

be maintained in captivity with substitute foods. Through limited experiments, we sought answers to these questions.

MATERIALS AND METHODS

Atlantic menhaden larvae used in the laboratory studies were caught in the mouth of the Newport River, N.C. The experiments were made at BCF Biological Laboratory, Beaufort, N.C., in January and February 1961.

Capture and Establishment of Larvae

Our proposed experiments hinged on our capability in collecting and establishing viable Atlantic menhaden larvae in the laboratory. Larvae were caught with 1-m.-diameter nylon plankton nets (mesh aperture 0.90 mm.) suspended in flooding tidal currents. A wooden pen (1.4 by 0.9 by 0.4 m.), lined with plastic window screen (mesh aperture 1.50 mm.), was attached to the cod end of the net. This arrangement reduced the mortality sometimes associated with capture of fish larvae (Marr, 1956). The catches were dipped from the pen with 9-liter plastic buckets and transported therein to the laboratory (fig. 13). Menhaden larvae were removed, one or two at a time,

FIGURE 13.—Capture of Atlantic menhaden larvae.

from the buckets in 100-ml. beakers and placed in laboratory aquariums. By these techniques menhaden larvae were kept immersed at all times and could easily be separated from larvae of other species.

Two porcelain bathtubs served as laboratory aquariums. To minimize the bumping of the newly captive larvae against the tub walls, the interior was painted black and illuminated continuously by pink fluorescent lamps mounted 2 m. above the water. Filtered sea water was continuously supplied to each aquarium and the level controlled by a 10-mm.-diameter standpipe to provide a volume of 180 liters for about 300 larvae, 13 to 28 mm. long. During the establishment period, salinity varied between 28 and 33 p.p.t. (parts per thousand) and temperature, between 16.0° and 19.0° C.

The larvae were left undisturbed for at least 12 hours after transfer to the laboratory aquariums. Dead or dying larvae were removed daily. Total mortality during establishment was less than 5 percent.

Experimental Procedures

Experiments were begun 3 to 5 days after larvae were established in the aquariums. Individual tests were made in 100-ml. beakers, 250- and 500-ml. bowls, or 8-liter battery jars, all painted black, and filled with sea water from the aquarium supply. Larvae were transferred to the test container with a 100-ml. beaker, one or two specimens at a time. From 1 to 10 larvae were placed in each beaker or bowl and as many as 20 larvae in each battery jar.

Procedures differed for specific studies. They are described separately.

Light and feeding.—Larvae were transferred to 250-ml. bowls, eight larvae to a bowl, and left unfed in total darkness for 24 hours before the experiments were started. *Artemia* nauplii in suspension were dropped into the bowls (*Artemia* were used in preference to copepods because their pink color made them readily distinguishable after ingestion by the larvae). Light intensity of a 500-watt, tungsten filament lamp suspended 75 cm. above the water was varied by a transformer and measured with a light meter at the surface. We used penlight illumination periodically to detect the presence of food in larvae kept in darkness or exposed to low light intensities.

Food passage and digestion.—Food ingestion and digestion times were determined visually and with a radioactive tracer. For the visual observations, several lots of eight larvae each were placed in 500-ml. bowls. They were left unfed for 24 hours before the start of the experiments and then fed *Artemia* nauplii. When they had stopped feeding, the larvae were transferred to separate 100-ml. beakers for observation. Rate of food passage was estimated from the time that feeding stopped until the alimentary tract of each larva was completely empty.

For the radioactive tracer tests, several lots of eight larvae each were placed in 500-ml. bowls and fed 10 to 50 copepods (*Centropages* and *Acartia*) that had been immersed in sea water containing 0.001 μc./ml. (microcurie per milliliter) of Zn^{65} and rinsed in fresh sea water before they were fed to the larvae. When the

larvae had stopped feeding (usually within 20 minutes), they were siphoned from the bowls, rinsed in fresh, nonradioactive sea water, and placed in separate 100-ml. beakers of fresh sea water. The radioactivities of each lot of copepods, of each larva (after rinsing), and of the sea water in each 100-ml. beaker were measured with a gamma-ray scintillation detector and a well-type 76-mm. sodium iodide crystal. The number of copepods ingested by an individual larva was estimated by dividing its net activity gain (counts per minute) after feeding by the mean count per copepod for the lot fed (attempts to feed an individual larva a single, radioactive copepod were unsuccessful). The presence of copepods in the alimentary tract was also verified visually at the time a larva was transferred to a 100-ml. beaker. Uptake and initial distribution of Zn^{65} in the body of larvae were followed over a 3½-day period. When a larva was killed (or died), the entire alimentary tract was removed, and its activity level and that of the remaining body tissues were determined.

Capture and preservation of larvae.—Three lots, each with eight larvae, were transferred to separate 500-ml. bowls and fed *Artemia* nauplii. After the larvae had stopped feeding, four of them were individually removed from one bowl with a 50-mm.-diameter nylon mesh dip net and placed in solutions of 0.4, 10, and 50 percent Formalin and saturated chloral hydrate respectively. The remaining four were first anesthetized by adding a solution of tricaine methanesulfonate (0.25 g./l.) to the bowl and then transferred in a similar manner. Larvae in the second and third bowls were divided and transferred to the same four solutions from bowl two by siphoning with a 25-mm.-bore plastic tube and from bowl three by dipping with a 100-ml. beaker.

FEEDING BEHAVIOR AND RESPONSES OF LARVAE TO SELECTED STIMULI

Feeding

Atlantic menhaden larvae are selective carnivores and voracious feeders. On transfer to a bowl, they schooled and began to swim slowly around the container. When an aqueous suspension of copepods was added to the bowl, the larvae scattered, but within 1 or 2 minutes they reformed in a tighter school and swam around the container at a faster rate than previously. Feeding began when an individual larva swam away from the school, slowed down, oriented slightly below and about 10 mm. away from a suspended copepod, flexed its body in an S-shaped position (fig. 14), and drifted within 2 to 5 mm. of the prey; then, with a sudden flip of its tail, the larva straightened out as it lunged forward and upward to engulf the copepod. After the "strike," momentum carried the larva a few millimeters beyond the point of capture, from whence it swam vigorously downward, completing an arc, and then returned to the original swimming depth before finally rejoining the school. The time required for an individual feeding act and return to the school was 3 to 5 seconds. If the copepod were missed, or only partly engulfed on the first try, the larva made several violent lunges in an attempt to seize it. If these attempts were unsuccessful, the larva swam

FIGURE 14.—Atlantic menhaden larva in the act of capturing a copepod. The body is flexed in an S-shaped attitude about 10 mm. from the prey and ingestion accomplished by a forward darting movement.

rapidly toward the school and rejoined it. Some larvae ingested as many as 15 copepods (average 10) before they stopped feeding. They ignored or rejected *Artemia* or *Balanus* nauplii, dead copepods, chopped clams, and finely ground particles of fish meal when introduced with copepods, but readily ingested *Artemia* or *Balanus* nauplii alone. Unsuccessful attempts at feeding and the occurrence of larvae with empty alimentary tracts during our observations suggest that some individuals may be inefficient feeders when the food supply is limited. Atlantic menhaden larvae thus appear to select preferred foods visually but will accept substitutes when no preferred foods are present.

Prejuveniles and juveniles reacted differently than larvae to the introduction of food. A school of fish suddenly reduced its forward swimming speed and turned in the direction of the food. Individuals differentially increased their swimming speed until they were in contact with the food; then, with mouth agape, they swam slowly upward and downward through the water as they appeared to suck in the food particles. Throughout feeding, their opercula were flared and their bright red gill filaments were clearly visible. At times some of the prejuveniles pursued individual copepods, but, in general, their feeding behavior was the same as that of juveniles. During feeding the fish spread out, but as the food supply diminished they gathered in small groups. These groups, enlarged by the addition of individuals, eventually joined to reestablish the school.

Our observations generally agree with those of Breder (1959), but indicate that filter feeding, rather than particulate feeding, is the principal means by which both prejuvenile and juvenile Atlantic menhaden obtain food.

Influence of Light on Feeding

Larvae fed at a minimal light intensity of 25 lux (table 9). At lower intensities, the larvae remained inactive and randomly distributed near the bottom of the bowl. At higher light intensities, the rate of feeding was increased and maximum intensity (about 500 lux) had no apparent adverse effect. We did not study the possible effects of the changes in wave length that accompanied reduction of light intensity on the feeding response.

Our laboratory observations thus indicate that Atlantic menhaden larvae do not feed at low intensities of artificial light; however, results of our field studies suggested that larvae fed more actively on moonlit nights than on dark nights. The incident light intensity of moonlight probably does not exceed 0.5 phototopic lux (Urey, 1961), but this natural light level may be sufficient for larvae to capture swimming copepods silhouetted at or near the water surface.

TABLE 9.—*Numbers of larvae feeding at different light intensities*

[Light intensities in parentheses]

Elapsed time following introduction of food	Larvae with food in alimentary tract					
	Lot 1		Lot 2		Lot 3	
Minutes	*Number*	*Lux*	*Number*	*Lux*	*Number*	*Lux*
0	0	(0)	0	(25)	0	(8)
15	0	(0)	8	(25)	0	(8)
30	0	(0)	----------		[1]3	(25)
45	0	(0)	----------		[2]8	(25)
60	0	(4)	----------		----------	
70	0	(4)	----------		----------	
80	0	(8)	----------		----------	
160	0	(15)	----------		----------	
195	[1]6	(25)	----------		----------	
210	[2]8	(25)	----------		----------	

[1] Feeding began.
[2] Alimentary tract full or nearly full.

Digestion Time

Artemia nauplii passed through the esophagus to the posterior alimentary tract—where they often could be seen wriggling—within 1 to 3 seconds. At water temperatures ranging from 16.8° to 17.5°C., 80 percent of the larvae with apparently full posterior tracts had voided all contents between 8 and 10 hours after feeding; those estimated to be one-quarter to three-quarters full, between 6 and 7 hours. One larva retained food for 14 hours.

Rapid uptake of radioactive zinc (Zn^{65}) by the body tissues of larvae fed labeled copepods indicated that assimilation of food began almost immediately. Nearly two-fifths of the radioactivity was in the body tissues within 1½ hours; three-fourths, after 8½ hours; and

nine-tenths, after 34 hours (table 10). The total radioactivity decreased rapidly during the first day after the larvae were transferred to nonradioactive sea water (fig. 15). Between 17 and 19 percent of the Zn^{65} was retained within the body 14 days after feeding (no correction was made for Zn^{65} decay).

These findings suggest to us that digestion rate in relation to time since last feeding probably contributed to the low incidence of food found in larvae captured at Indian River Inlet during dark nights, and especially in those captured toward dawn.

TABLE 10.—*Distribution of Zn^{65} in Atlantic menhaden larvae after feeding on copepods labeled with this radionuclide*

[Levels represent the mean of individual lots of larvae, adjusted for the dosage given]

Elapsed time since feeding	Activity level	
	Alimentary tract	Remainder of body
Hours	*Percent*	*Percent*
0.0	98	2
1.5	59	41
8.5	24	76
34.0	10	90
89.0	1	99

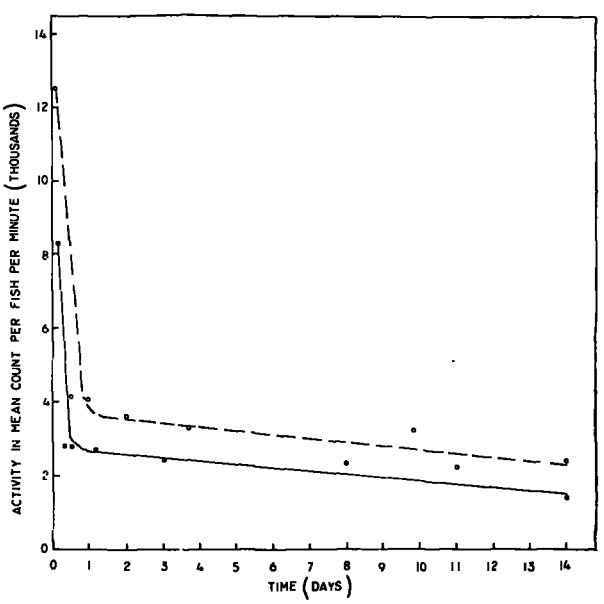

FIGURE 15.—Activity level of Zn^{65} in the body of Atlantic menhaden larvae fed labeled copepods and returned to nonradioactive sea water. Solid and open circles represent two larvae.

Effects of Capture and Preservation of Larvae on Their Alimentary Tract Contents

All larvae transferred by the dip net defecated all or a portion of their alimentary tract contents when removed from the water, but none transferred in sea water defecated any of their tract contents.

Active larvae placed in the various Formalin solutions had violent spasms, accompanied by complete or partial defecation of their tract contents. If defecation were incomplete, the remaining organisms were restricted to the end of the posterior alimentary tract. Sometimes the entire contents were ejected in a single, violent spasm. Generally, larvae voided their tract contents violently and completely in 10 and 50 percent Formalin and died within 10 to 30 seconds. In 0.4 percent Formalin they quivered for as long as 10 minutes and often defecated all or part of their tract contents.

Larvae placed in the chloral hydrate solution reacted as in the stronger Formalin concentrations, although they voided only about one-fourth to one-half of the tract contents.

Larvae in the tricaine methanesulfonate gradually lost equilibrium in 3 to 5 minutes and had no spasms. They did not defecate any portion of their alimentary tract contents during transfer by net or immersion in Formalin or chloral hydrate.

These observations suggest that larvae may defecate much of their alimentary tract contents during capture with a net or at the time of preservation, thereby leading one to the erroneous conclusion that they feed little or digest their food rapidly. So both the high incidence of empty alimentary tracts and the low numbers of food organisms per tract which we found in larvae collected at Indian River Inlet probably was largely due to the harsh treatment to which larvae were subjected during retrieval of the net from the water onto a bridge (about 10 m. above the surface) and their preservation in Formalin. Capturing larvae with a net attached to a floating pen and anesthetizing them prior to preservation should provide specimens with alimentary tract contents that reflect actual conditions at the time of capture.

REARING YOUNG MENHADEN IN THE LABORATORY

The foregoing field and laboratory studies provided the necessary technical information for us to establish and successfully rear Atlantic menhaden larvae through and beyond metamorphosis in captivity. Feeding was begun about 12 hours after larvae were established in an aquarium. The maintenance ration was varied according to the developmental stage of the fish. Larvae were fed a daily ration of 15 to 20 copepods (chiefly *Centropages* and *Acartia*, 0.5 to 1.3 mm. greatest dimension) or 30 to 50 *Artemia* nauplii per larva. At the onset of metamorphosis, the animal diet was supplemented with natural phytoplankton pumped into the aquarium from nearby intertidal waters. The pumping rate was adjusted to provide a daily minimum of 17 liters of water per fish. After metamorphosis was completed, a slurry consisting of 10 parts menhaden meal and 1 part pureed clam (*Mercenaria mercenaria*) was substituted for the copepod-*Artemia* nauplii component and fed at a ratio of 1 to 20, based on the total estimated weight of the fish in an aquarium.

The handling and feeding procedures described in this paper can provide healthy stocks of young menhaden in different developmental stages for laboratory research.

SUMMARY

This paper covers the food of young Atlantic menhaden, changes in the alimentary tract and related body structures during their metamorphosis from larvae to juveniles, and laboratory studies of feeding, digestion, and associated responses of the young fish.

The alimentary tracts in 592 Atlantic menhaden larvae collected at Indian River Inlet, Del., were examined for food. More than half of the tracts were empty. Contents of 243 tracts that contained food consisted almost entirely of copepods, chiefly *Centropages*. Generally, larger larvae fed on larger copepods, and greater numbers of copepods in tract contents were associated with daylight and evening hours. Food items generally reflected the composition and relative abundance of individual copepod genera in the plankton. Although phytoplankters were abundant at the Inlet, larvae did not eat them.

Young menhaden changed their food habits during metamorphosis within the estuary. Alimentary tract contents of 20 larvae and 31 early-stage prejuveniles consisted almost entirely of copepods, chiefly *Acartia*. Tract contents of late-stage prejuveniles and juveniles consisted mostly of pennate and centrate diatoms, dinoflagellates, and amorphous plant materials. In general, major food items identified in the alimentary tracts also were the more abundant organisms in the water.

Metamorphosis of Atlantic menhaden is distinguished by the development of a highly specialized gill raker-alimentary tract complex. The mouth is relatively large at all stages of development. Prominent maxillary and dentary teeth are present in larvae. The teeth become nonfunctional during late metamorphosis and eventually disappear. Gill rakers are rudimentary in larvae, but increase in length, number, and complexity during metamorphosis. Pharyngeal pockets appear during metamorphosis. The alimentary tract of larvae is nearly a straight tube. In prejuveniles the tract begins to fold forward, the muscularized stomach (gizzard) starts to develop, and many pyloric caeca become evident. In juveniles the intestine forms several coils, pyloric caeca increase in number and length, and fat deposits usually surround the caeca and lie between the folds of the intestine.

Observations on Atlantic menhaden in captivity confirmed that larvae and early-stage prejuveniles feed selectively on living prey. They capture their prey by flexing and striking like a snake. An individual larva may ingest as many as 15 copepods, but the average was 10. Larvae preferred copepods, but also fed on *Artemia* and *Balanus* nauplii. Late-stage prejuveniles and juveniles feed mainly by filtering plankton in the water. They disperse while feeding, but reassemble in a tight school when they have exhausted the food supply.

Laboratory studies of selected responses of Atlantic menhaden larvae suggest that the absence or low numbers of food organisms found

in the alimentary tracts of larvae collected at Indian River Inlet may have been largely due to their defecating all or part of the contents during capture and preservation. Proper capture devices for larvae and their anesthetizing prior to preservation should reduce loss of their alimentary tract contents. Other factors which may have contributed to the paucity of food in alimentary tracts were lower feeding rate during dark nights and digestion rate in relation to elapsed time since last feeding.

Information obtained from our studies enabled us to establish and successfully rear Atlantic menhaden from larvae to juveniles in captivity. The work also provided insight into some aspects of the estuarine ecology of young Atlantic menhaden.

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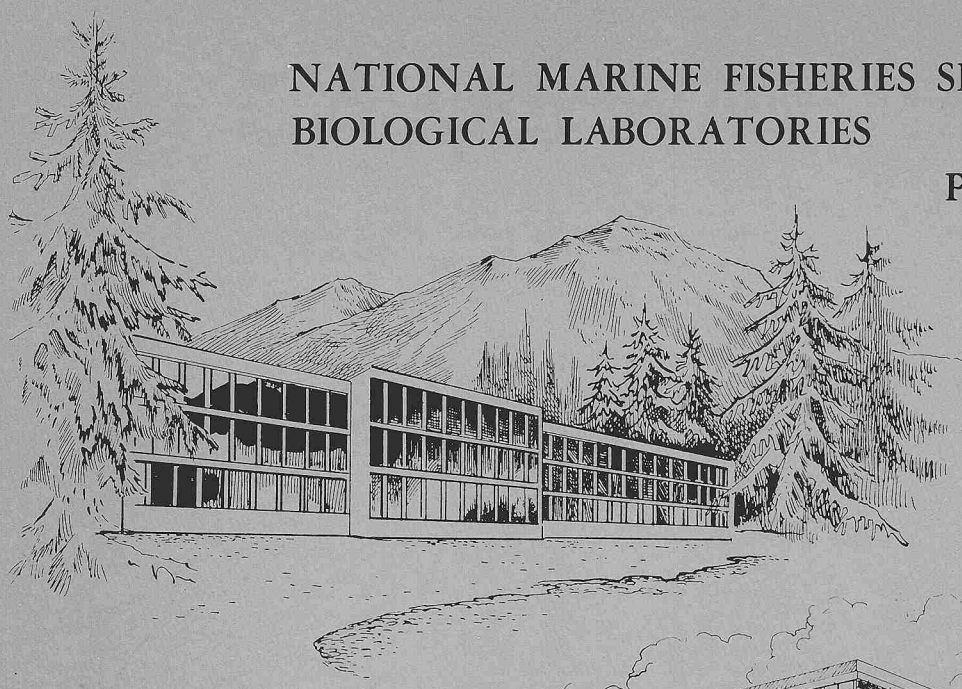

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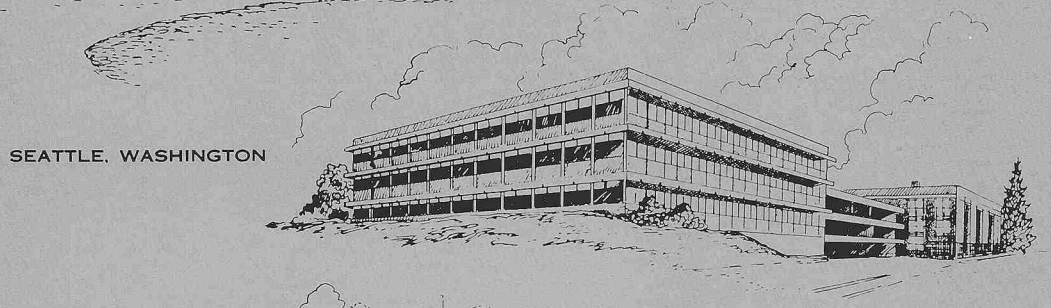

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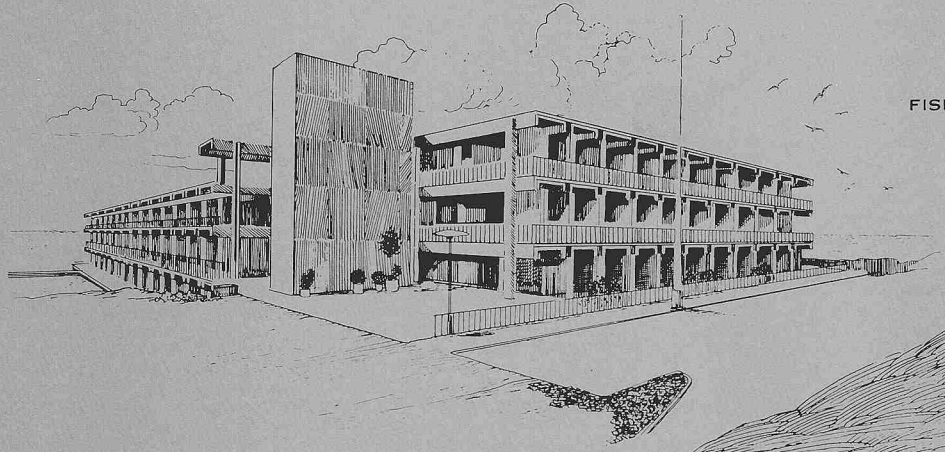

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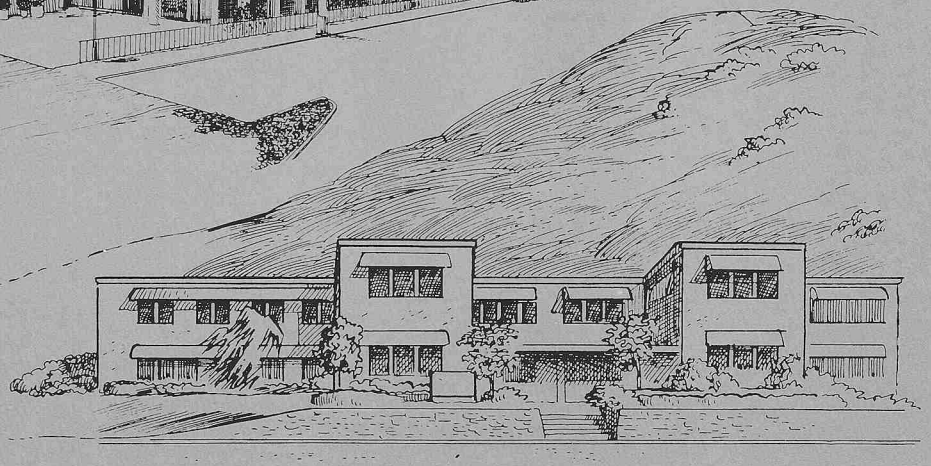

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