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BUREAU OF COMMERCIAL FISHERIES

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AGE AND GROWTH OF THE REDFISH
(*SEBASTES MARINUS*)
IN THE GULF OF MAINE

By GEORGE F. KELLY AND ROBERT S. WOLF



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ABSTRACT

Validity of the use of the otolith in age-growth studies of the redfish (*Sebastes marinus*) is demonstrated. Otoliths accrue one opaque and one hyaline band a year. The opaque band begins to form in April, the hyaline band in September. Otoliths preserved in ethanol may be read whole, although those from larger fish are more easily read after they are sectioned. Otoliths stored dry must be sectioned for reading.

Redfish larvae can be collected in surface waters throughout the period of spawning, April to September. The fry descend into mid-depths as they grow and first appear on the bottom in August. Redfish reach an average length of about 50 mm. in their first year of life.

The sexes grow at virtually the same rate until the tenth year, after which the male grows more slowly than the female. Redfish of the Gulf of Maine grow more slowly than those of northern European waters.

While dominant age classes appear in the collections of young fish, they are not obvious in samples of older, commercially available fish.

AGE AND GROWTH OF THE REDFISH (*SEBASTES MARINUS*) IN THE GULF OF MAINE

By GEORGE F. KELLY AND ROBERT S. WOLF. *Fishery Research Biologists*
BUREAU OF COMMERCIAL FISHERIES

The redfish of the Gulf of Maine, *Sebastes marinus* (Linnaeus), has supported an economically important fishery in the United States since the late 1930's. The fishery has played a major role in the livelihood of several New England ports, particularly Gloucester, Mass., and Rockland and Portland, Maine. Redfish fillets have found a ready market in this country and, lately, in many European countries as well. The fishery developed, as have so many others, first in local waters, gradually moving out farther and farther as the closer fishing grounds became less profitable and as gear and techniques improved. Vessels hailing from New England ports now fish as far away as the waters off Labrador. The redfish is also sought after by many European fishermen on the shelf areas of much of the boreal North Atlantic. The vessels of Soviet Russia and Germany have fished for this species from the northern coast of Russia itself to certain isolated fishing grounds off the coast of Canada. This intensive effort has underscored the urgency of understanding the life history of the species.

Sebastes marinus, the redfish or rosefish, belongs to a North Atlantic species-group that is not well understood taxonomically at this time. *Sebastes marinus* (Linnaeus) and *S. viviparus* Kroyer are generally accepted as the only valid species of the genus. The status of *S. mentella* Travin (1951) is not firmly established. Andriiashev (1954) has questioned the validity of the species, stating that of the characteristics used to separate *mentella* from *marinus*—

all were poor transient characters or showed only average differences . . . these forms were distinguished by insufficient investigation over the extent of their broad range (to the Faeroe Islands, Iceland, Greenland, and the shores of the U.S.A.).

Andriiashev accordingly reduced *mentella* to the status of a subspecies of *marinus*.

Whatever its taxonomic structure, the group in general has been studied by many people in this country and abroad. The importance of

this fishery at the international level has greatly increased the amount of research being done, and a particularly spirited controversy has developed about the radically different growth rates derived by various workers. This paper is primarily concerned with the growth rate of the redfish population in the Gulf of Maine. It is to be hoped that the results of this research will have wider application; in any event, this information is necessary for the proper evaluation of the New England redfish fishery.

BRIEF REVIEW OF THE LITERATURE

1880. R. Collett, working on collections made in the Bear Island-Spitzbergen area by the Norwegian Atlantic Expedition of 1876, reported that redfish fry were about 6 mm. long at birth.

1922. Ad. S. Jensen reported on the extensive observations that he made on redfish in West Greenland waters in 1908-9. He collected redfish fry periodically from the time of the first appearance in the plankton, recording the changes in size composition for the first 9 months of life. His data indicated an average length of 5.5 cm. for fish 8 to 9 months of age. He attempted to estimate a growth rate of the redfish from length-frequency data. This particular population ranged from 7 to 71 cm. in length. He suggested that fish in age-group I ranged from 7 to 17 cm. in length, in age-group II from 19.5 to 30 cm. in length, and in age-group III from 31 to 41 cm. in length.

1936. N. P. Smaragdova is to be credited with the first detailed study of the age and growth rate of *Sebastes*. He referred his species to *S. marinus*. His work was based on scales, although he did make a comparative study of scales and otoliths. The material came from the Barents Sea and was collected over a period of 12 years, 1921 to 1932. He reported good agreement between age readings made from scales and those made from otoliths. He concluded that the

redfish is relatively slow growing and long lived. He estimated the length at 1 year to be 5.4 cm. The oldest fish in his collection, with an estimated age of 27 years, measured 57 cm. in length. The data presented by Smaragdova are somewhat erratic but do not differ greatly from that of later workers.

1944. V. V. Veschezerov also studied the age and growth of redfish from the Barents Sea. He used otoliths to estimate the age of 764 fish ranging in length from 3 to 63 cm. He concluded, as had Smaragdova, that the Barents Sea redfish are relatively slow growing and that some of his fish were as old as 26 years. He estimated the length at 1 year to be 5.1 cm. The largest fish, 58.3 cm. in length, was estimated to be 24 years old.

1949. A. Perlmutter and G. M. Clarke published a detailed study of the growth rate of *S. marinus* in the Gulf of Maine and off western Nova Scotia based on age readings obtained from the scales. The study was deliberately aimed at immature fish, or fish less than 23.5 cm. in length. The rate of growth arrived at was comparable to that published by Smaragdova for the Barents Sea population of *S. marinus*. The data suggest that redfish mature at about 8 to 10 years of age and are very slow growing.

1951. V. I. Travin published growth data for *S. marinus* from the Barents Sea in a paper that also described a new species of redfish, *S. mentella*. *S. marinus* was described as being restricted to depths of less than 300 meters, whereas the new species occurred to depths in excess of 300 meters. *S. mentella* Travin is described as having a slower growth rate than that of *S. marinus*. Unfortunately, the growth data for both species are presented simply as average lengths at age without information on the number of fish involved or the method used to age the fish. Travin's growth data for the two species indicate that they grow at about the same rate until 4 years of age, after which *mentella* grows more slowly than *marinus*. At 17 to 18 years of age, *marinus* averages 8 to 9 cm. longer than *mentella* of the same age. His data suggest slightly faster growth than that implied by the data of Veschezerov and Smaragdova for fish up to about 14 years of age. His largest fish, 49.9 cm. in length, was estimated to be 18 years of age. Fish estimated at 18 years by Veschezerov averaged 50 cm. in length, while

those considered to be 18 years old by Smaragdova averaged 44.9 cm.

1952. A. Kotthaus, working with material from the coast of Norway and from the Bear Island region, presented very rapid growth rates, which resulted from his conclusion that the redfish developed three sets of hyaline and opaque bands a year on the otolith. His studies were based on nearly 15,000 fish, ranging from 11 to 81 cm. in length. He considered that the modes of the length frequency curve of his entire sample represented the first seven year classes. While we disagree with Kotthaus' conclusions, it must be admitted that his findings are provocative and stimulating.

1953. H. B. Bigelow and W. C. Schroeder state that the redfish is a "very slow growing fish." Their opinion is based on Perlmutter and Clarke's study and on some specimens they had collected that averaged 2½ inches and were considered to be about 1 year of age.

1956. E. Bratberg published a careful study validating the use of scales and otoliths for determining age of redfish. He collected 19 samples of small redfish regularly from three localities along the coast of Norway for a period of 18 months. Bratberg examined a total of 1,860 specimens ranging in length from 5.5 to 22 cm. He demonstrated that only one opaque and one hyaline band is formed in any one year. The periphery of the otolith is opaque from May through September and hyaline from October to April. Although he worked mostly with younger fish, he presented growth data for fish up to and including age 7.

To sum up, with the notable exception of one study, the various published growth data demonstrate general agreement that *Sebastes* species grow very slowly. Whether or not it develops in the future that one or many species are involved, much of the research accomplished to date indicates less variation in the results of different workers than has been observed many times between closely related populations of other species of fish. The data that will be presented in this paper and that presented by Perlmutter and Clarke (1949) strongly suggest a significantly slower growth rate for the Gulf of Maine stock than that reported for the redfish in the Barents Sea and along the coast of Norway.

OBJECTIVES AND METHODS

The primary objective of this paper is to present age-growth information on the redfish population of the Gulf of Maine. This information was needed for the intelligent planning of our research program which is, of course, concerned with determining how this valuable fishery should be managed.

To attain our objective, it was necessary to interpret the banding of the otolith. Related to this was the question of when the first annulus was completed in the otolith. Some difficult problems associated with growth during the first year of life had to be solved. With verified age-growth data available, it was finally necessary to determine the age composition of samples from the redfish population of the Gulf of Maine.

These several problems were approached in many ways. It was decided, after due consideration of the scale markings, to use otoliths for the age-composition studies. The samples were largely obtained from the commercial catches. For the detailed study of the otolith and the seasonal nature of its bands, a special station for sampling small redfish was selected and occupied at appropriate intervals.

SAMPLING THE COMMERCIAL CATCH

Since large quantities of redfish are landed at Gloucester, Mass., and Portland and Rockland, Maine, the bulk of the sampling was performed at these ports. Port samplers removed the otoliths from random samples of 25 fish each from those catches that came from single statistical subareas (Rounsefell 1948). The otoliths were stored dry in separate small paper envelopes on which were recorded the fork length and sex of the fish along with the necessary interview information. These samples were sent to the Woods Hole laboratory for preparation and reading.

SAMPLING BY RESEARCH VESSELS

To augment the sampling of the commercial catch, the R/V *Albatross III* and a chartered small commercial vessel, the M/V *Priscilla V*, were used to collect material. Whenever possible all such collections were made on well-known fishing grounds. These collections provided us with the necessary samples of the smaller sizes of redfish not landed in the commercial catch. A considerable amount of general survey work

has also been done with an Isaacs-Kidd midwater trawl (Isaacs and Kidd, 1951).

Certain aspects of our research required large samples of very small redfish. This material was collected at a special fish-sampling station off Cape Ann, Mass., where such small redfish could be obtained in number throughout the year. Designated the New Scantum station (*see* U.S. Coast and Geodetic Survey Chart 71), it is located 42°42' north latitude, 70°11' west longitude. Every effort was made to keep the collecting activities within 5 miles of this point.

PREPARING THE OTOLITH

Redfish otoliths, particularly those of smaller fish, may be easily read without any preparation. Otoliths removed from fresh fish or frozen fish may be stored indefinitely in 95-percent ethanol without loss of clarity. For this reason, it became standard procedure aboard the research vessels to slit and preserve in alcohol all fish less than 15 cm. in length. It was not convenient to preserve quantities of larger fish in this way; instead they were frozen. Their otoliths were removed in the laboratory after the fish thawed and were then preserved in alcohol.

Most of the otoliths used in this study were collected from the commercial catch. These were stored dry. Dry otoliths cannot be read whole, but must be sectioned. They were cut with a dull razor blade across the long axis just to one side of the focus. Using slight pressure, the blade was sawed across the otolith, causing the otolith to break into two pieces along the line of cutting. The exposed face, a cross section of the otolith, was polished with a high-speed carborundum cutting disk.

READING THE OTOLITH

The otoliths stored in alcohol were read as whole mounts and needed no further preparation. The whole otolith was placed in a small watchglass filled with 60-percent alcohol and examined directly with a binocular microscope. The watchglass was coated on the outside with black lacquer to provide a contrasting background.

The sectioned otoliths were placed in a slotted cork, polished face up, for examination with a binocular microscope. A lamp provided the necessary illumination along the side of the otolith. The polished face was shaded from direct lighting

with an opaque shield so that light was transmitted up through the otolith from below. The hyaline zones show up as bands of light, when so illuminated, contrasted against an opaque background. In similar manner, the number of light (hyaline) bands were counted from the center to the outer edge along the longest axis of the face. With a little experience, one soon learns to shade the otolith correctly and to position it properly in the path of light for the greatest ease of reading. As might be expected, the outer zones of large otoliths are narrower and more difficult to count accurately than are those of smaller otoliths.

No differences could be detected between each of the otoliths from a single fish; one of the pair was selected for whatever job was at hand without any consideration being given to whether it was the right or left otolith. In fact, the two otoliths of any pair were so much alike that almost anyone could separate out the pairs if a large number of pairs from one age group of fish were combined into a single sample.

STUDIES OF THE OTOLITH

SEASONAL NATURE OF BANDING IN OTOLITH

Our study of the formation of the bands in the otolith, like that of Bratberg (1956), was based on collections made from young fish. In all, 1,921 otoliths from 8 samples of fish collected over an 18-month period were examined to determine the nature of the material at the periphery of the otolith. The results of this study are presented in figure 1. We determined the percentage of otoliths with each type of material at the periphery, hyaline or opaque. The number of otoliths

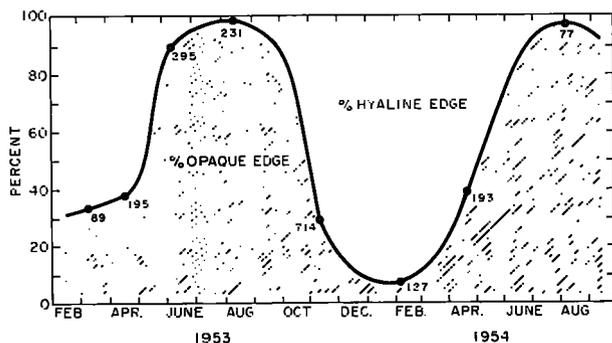


FIGURE 1.—Seasonal variation in the nature of the material at the periphery of the otolith of young redfish from the New Scantum station. Samples were composed of fish from pre-annulus to age-group VII. Figures on curve indicate number of specimens in each sample.

with an opaque margin is at a maximum during the months of July, August, and September. The number of otoliths with a hyaline margin reaches its maximum in January and February. The seasonal change is striking and unequivocal. There can be no question whatever about the annual nature of the banding in the otolith of the Gulf of Maine redfish. While it is more difficult to follow this sequence in the otoliths of older redfish, careful examination reveals no deviations from this general pattern. The outermost margin of any completed hyaline band may confidently be regarded as an annual ring and will be considered here as the annulus that marks the end of a year's growth.

In figure 2, a series of otoliths from the sample of 1,921 otoliths used in the analysis of the peripheral material are arranged by season and age group to demonstrate further the seasonal nature of the banding. Although photographs of material of this sort leave something to be desired, the gradual change in the nature of the peripheral band can be followed.

Bratberg (1956) went one step further. He demonstrated the concomitant formation of annuli on both the scale and the otolith, indicating that, in younger fish at least, comparable growth data may be derived from either scale or otolith.

COMPARING WHOLE MOUNTS AND CROSS SECTIONS OF OTOLITHS

The otoliths from a 7-year-old redfish are shown in figure 3. One otolith as it appears in a whole mount and the other in cross section following the preparation procedure outlined earlier. To determine the extent of agreement, comparative readings were made of whole mounts and cross sections of otoliths from 298 redfish ranging in length from 11 to 40 cm. The results are presented in table 1. There was 85-percent agreement between the two methods in those otoliths with less than nine annuli. The agreement is progressively poorer as the fish increase in length and age. The sample was not large enough to analyze these disagreements with any statistical validity.

COMPARING SCALES AND OTOLITHS

The pattern of annulus formation is the same in the scales and in the otoliths from the same specimen (fig. 4). The results of the age-reading comparisons of the scale and otolith from two

NUMBER OF YEAR-ZONES

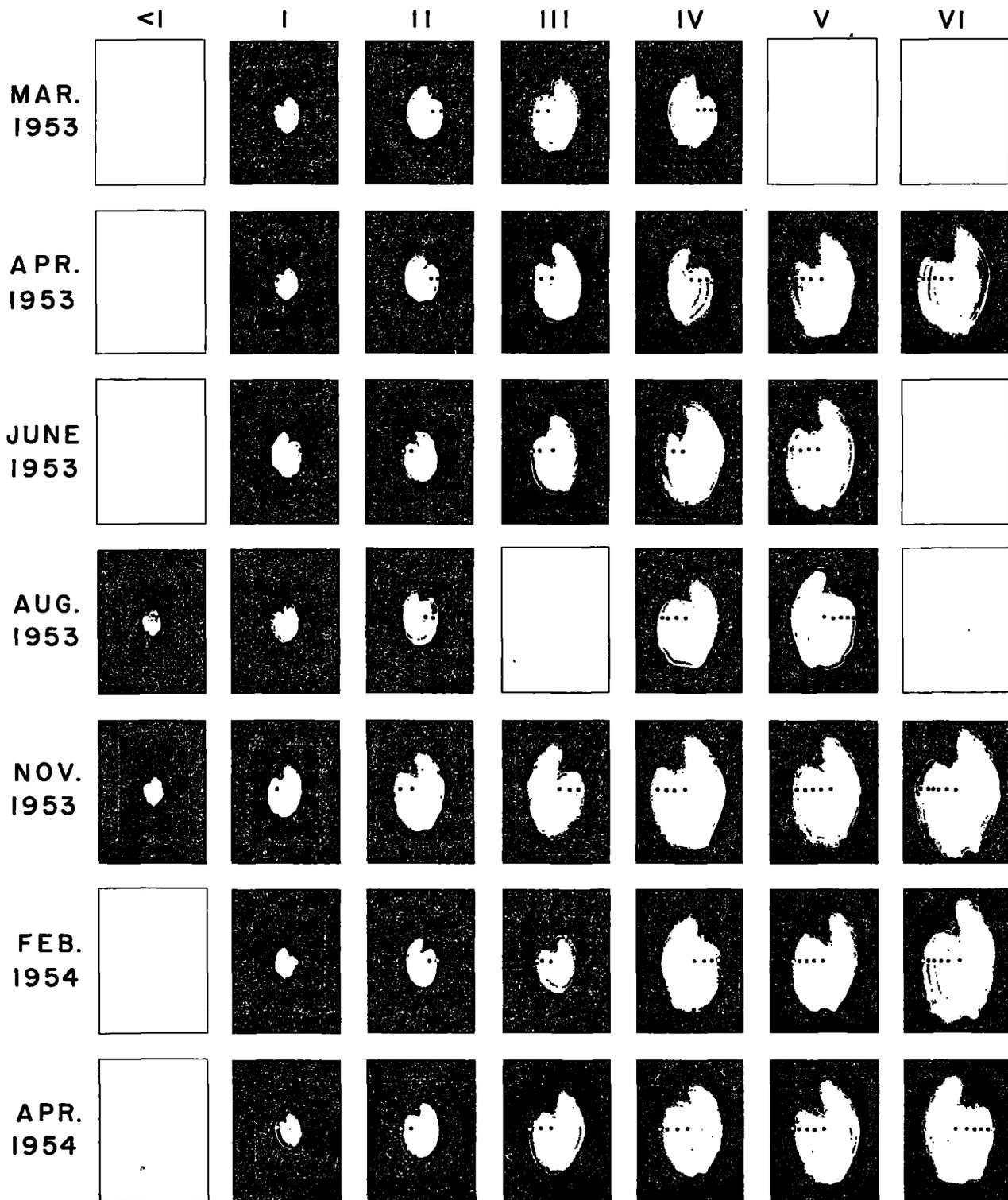


FIGURE 2.—Seasonal change in the peripheral material of the otolith of redfish, by age groups (pre-annulus to age-group VI), in collections from the New Scantum station. The black and white dots indicate the positions of the annuli.

TABLE 1.—Age-reading comparisons of pairs of otoliths from the same fish, one otolith cut, the other whole
 [Otoliths from 298 redfish from 11 to 40 cm. in length; collected April 19, 1953]

		WHOLE OTOLITHS																								Number of otoliths		
SECTIONED OTOLITHS	Number of annuli→	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24			
	1																											
	2																											
	3			1																								1
	4				22	1																						23
	5				2	90	4																					96
	6					10	45	3	1																			59
	7						4	26	1																			31
	8							3	6			1																10
	9									3	4	2	1															10
	10										1	4	3	2	3													13
	11										1	2	1			1	1											6
	12											1	3	2	3	1												10
	13											1	2	2	1	1					1					1		9
	14										1		2	3	1		2	1	1									11
	15																			1	1							3
	16																			3								3
	17															1	1											2
	18																1											2
	19																			1	2							4
	20																1											2
	21																											1
	22																											1
	23																				1							1
24																										1	1	
Number of otoliths			1	24	101	53	32	11	6	11	9	8	11	4	3	5	5	6	2		3	1	1	1	1	1	298	

TABLE 2.—Age-reading comparisons of scales and otoliths from young redfish collected at the New Scantum station in 1953

A. Scales and otoliths from 134 fish, 5-15 cm. in length, collected March 11, before new growth had started

B. Scales and otoliths from 201 fish, 5-11 cm. in length, collected April 20, after new growth had started

		SCALES						Unreadable scales	Number of scales
WHOLE OTOLITHS	Number of annuli→	1	2	3	4	5	6		
	1		5						5
	2		2	80					84
	3			1	10				11
	4				2	14	2	1	23
	5					1	9		10
	6							1	1
	Unreadable otoliths								
Number of otoliths		7	81	12	15	11	2	134	

		SCALES						Unreadable scales	Number of scales	
WHOLE OTOLITHS	Number of annuli→	1	2	3	4	5	6			
	1		9						1	10
	2			174		1			5	180
	3				1	6	1			8
	4						2			2
	5									
	6							1		1
	Unreadable otoliths									
Number of otoliths		9	175	6	4		1	6	201	

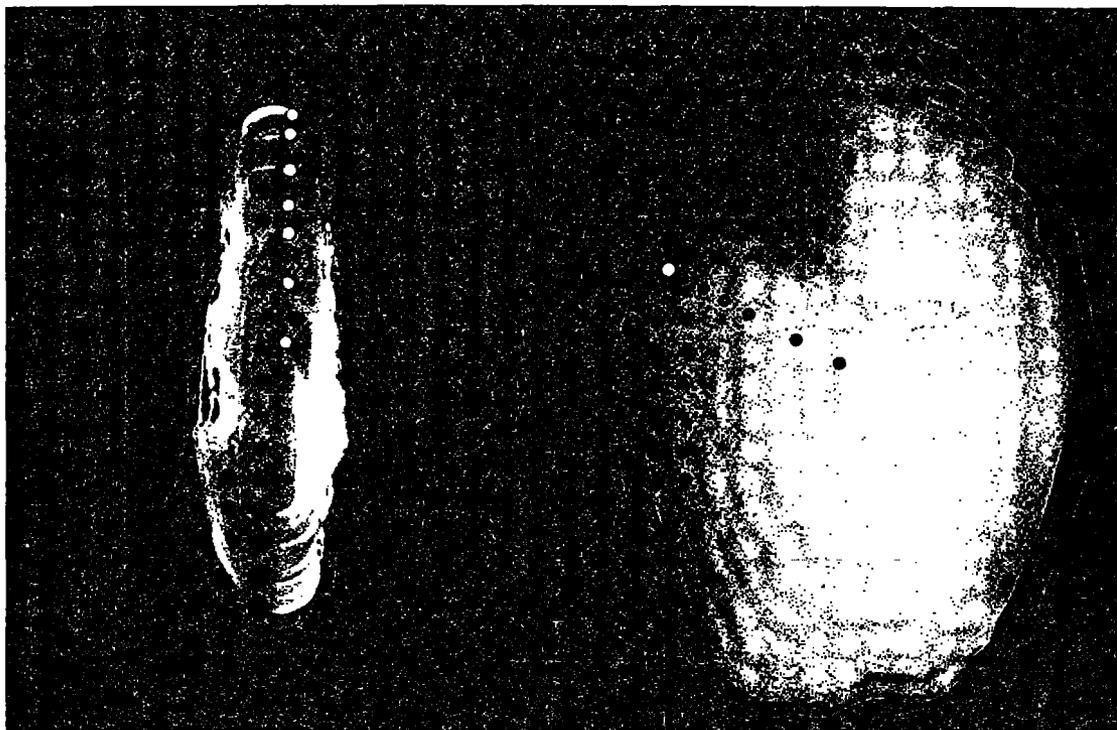


FIGURE 3.—Whole-mount and cross-section preparations of otoliths from an 18.1-cm. female redfish. Seven annuli are visible. Dots indicate hyaline zones.

samples of small redfish collected in March and April 1953, totaling 335 fish, are presented in table 2. The agreement is generally excellent, in one case being 88.8 percent and in the other 95.5 percent. In older fish, the scale annuli become progressively more difficult to distinguish with any certainty, so no attempt was made to run comparison tests in older age groups.

INDEPENDENT READINGS OF OTOLITHS

The number of annuli and the nature of the material at the periphery of the otolith can be determined from whole otoliths with up to at least nine annuli. Two readers independently determined this fact from a sample of 1,809 otoliths (table 3). They were in complete agreement on the annulus count and virtually in complete agreement as to the nature of the peripheral material.

The otoliths of larger fish become progressively more difficult to read as age increases. Three lots of 100 otoliths each from older fish (VII to XX+) also were read independently by two investigators. Thirty-one percent of the age readings agreed exactly, and 59.7 percent agreed to within 1 year. In a few instances, the readings deviated from

each other by as much as 9 years. The average agreement between readers for each of the lots was ± 1.16 , ± 1.87 , and ± 1.85 years. These data illustrate the difficulty of estimating accurately the age of older fish, and suggest the limits of reliability that can be placed on determinations of age of older redfish.

AGE AND GROWTH

Gravid female redfish are commonly found in April and the first of the newborn 5-mm. larvae may be collected at this time; redfish are born from then until September. The larvae quickly ascend to the surface layers of the ocean where they are taken in surface plankton tows. By mid-May, larvae as long as 12 mm. appear in the plankton, and by mid-June, postlarvae 20 mm. long may be collected. The young descend slowly as they grow, and for this reason the size range in the uppermost layers of the water shows little significant change throughout the spawning season. In March, April, and June, 1953, all otoliths from small redfish taken on the bottom had one or more completed annuli. The one-annulus fish ranged in length from 45 to 70 mm.,

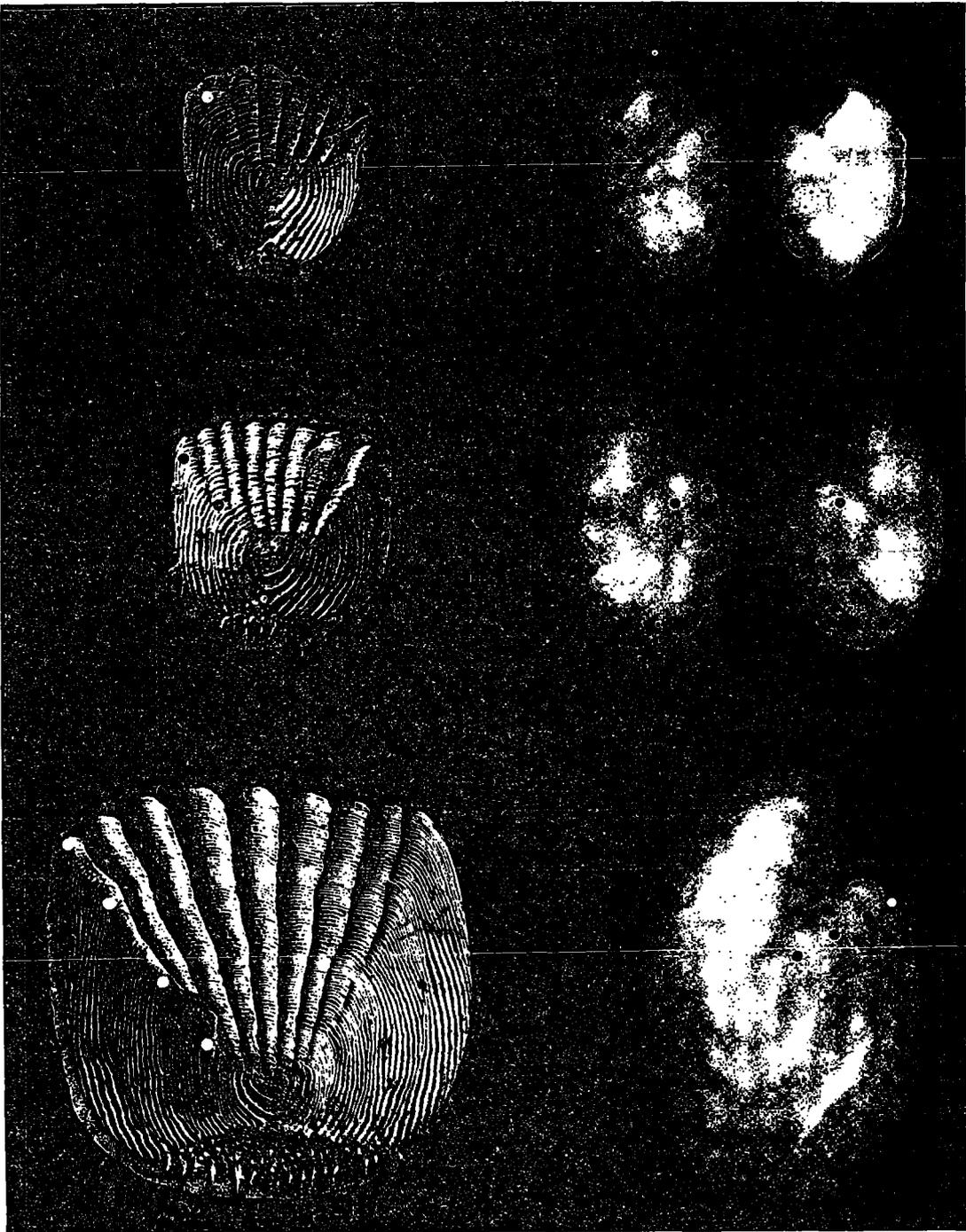


FIGURE 4.—Comparison of scales and otoliths from a 6.1-cm. female with one annulus (top row), a 6.9-cm. female with two annuli (middle row), and a 13.0-cm. male with four annuli (bottom row).

TABLE 3.—Comparison of age readings by two readers of otoliths from 1,809 redfish, collected at New Scantum station, August 17, 1955

[O=opaque; H=hyaline]

		READER A																		Number of otoliths		
Number of annuli→		O	H	O	H	O	H	O	H	O	H	O	H	O	H	O	H	O	H			
READER B	O																					
	H																					
	O			2																		2
	H																					
	O					368	3															371
	H						7															7
	O							1,043	7													1,050
	H								13													13
	O									27												27
	H										5											5
	O											126										126
	H												2									2
	O													194								194
	H														1							1
	O															9						9
	H																					
	O																			2		2
	H																					
Number of otoliths				2		368	10	1,043	20	27	5	126	2	194	1	9		2			1,809	

the two-annulus fish had a range in length of from 55 to 110 mm., while the three-annulus fish ranged from 80 to 120 mm. In the August collections of the same year, a group of fish 21 to 48 mm. in length appeared on the bottom, all of them with uniformly opaque (pre-annulus) otoliths. The periphery of these otoliths, however, showed signs of a developing hyaline edge. Most of these pre-annulus fish had some scales (fig. 5). None of the scales had developed an annulus. The first annulus, therefore, appears to be formed sometime between August and March, probably in late winter.

The scales begin to form first along the lateral line on the posterior half of the body. Redfish 34 mm. in length have been found with much of the posterior half of the body covered with scales (fig. 5). By the time that these small fish are about 40 mm. in length, they have acquired their full complement of scales.

GROWTH DURING FIRST YEAR

The conclusions of Perlmutter and Clarke (1949) concerning the growth of redfish in their first year

are reasonable on the basis of the material that they were able to collect and examine. They concluded that young redfish reach a length of about 20 mm. at the end of the first full year. It is, however, our opinion, as well as that of many European workers, that redfish reach 50 mm. or more in length during their first growing season. We believe this because the otoliths and scales of redfish up to about 50 mm. do not show an annulus, and because all of the material that we have analyzed indicates that these young fish reach an average length of 50 mm. in just a few months. We were fortunate in having at our disposal a large number of collections made by other workers. The length frequency data compiled from these collections, from our own collections, and from various published records, are presented in tables 4 to 11 and are illustrated in figure 6.

Redfish larvae are abundant in the surface waters throughout the spawning period. As the season progresses, the greater numbers of larger larvae in the plankton increase the average length slightly: from approximately 10 mm. in May to more than 20 mm. in early September. Young

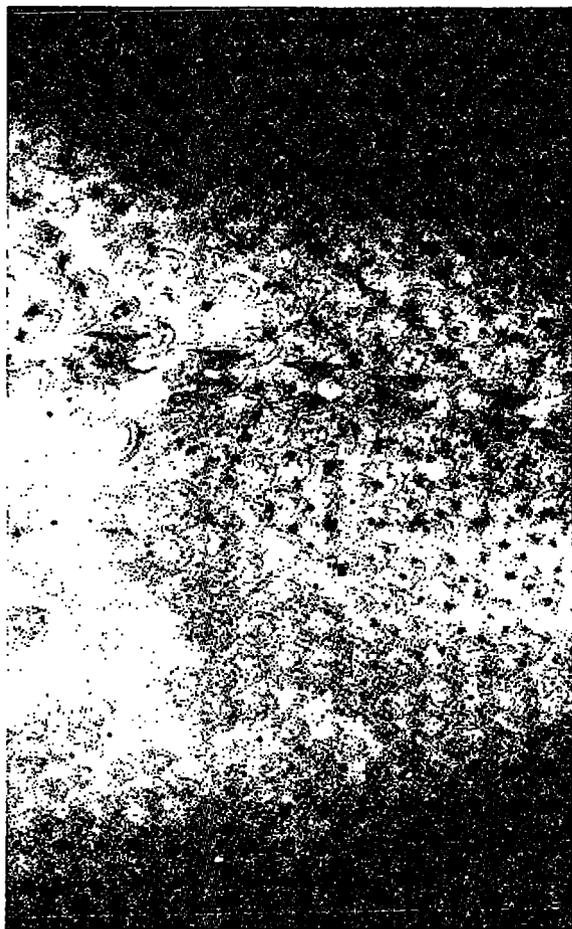


FIGURE 5.—Posterior portion of flank of a 34-mm. redfish, showing the newly formed scales. The scales along the midline have two or more circuli, while the smallest (and newest) scales on the dorsal and ventral surfaces have none or one circulus. Some scales were rubbed off when the fish was captured.

fish varying in length from 20 to 50 mm. appear on the bottom in August for the first time. There is a general lack of fish between 20 and 40 mm. in length in any of these collections. What material we do have leads us to conclude that the fish in this size range were probably somewhere between the surface and the bottom. Recent research, the results of which are not plotted on figure 6, has demonstrated that redfish slowly descend as they grow and that these 20- to 40-mm. fish may be found in the middepths. This particular phase of redfish early life-history will be discussed only briefly at this time.

Some very revealing samples of young redfish were collected at depths of 10, 20, 30, 40, 60, and 100 meters with the Isaacs-Kidd midwater trawl in August 1957 (*Albatross III* cruise 99). At this time, these fish varied from 10 to 40 mm. in length. At 10 meters, all lengths within this range occurred with the average being about 22 mm. The largest collections per tow, made at 20 meters, contained many times more specimens than all the rest of the tows at the other depths. The average length of this sample taken at 20 meters was 23 mm. At 40 meters and at 60 meters the samples were small, but the average length was slightly larger than the average length of fish at 20 meters. The length was approximately 27 mm. at a depth of 60 meters. Two tows at 100 meters failed to collect any young redfish. A similar cruise (*Albatross III* cruise 102) in September 1957 demonstrated the further growth and descent of the young. The largest samples per tow came from depths of 80, 100, and 110 meters. The average lengths varied from 34 to 40 mm. without any marked relation to depth.

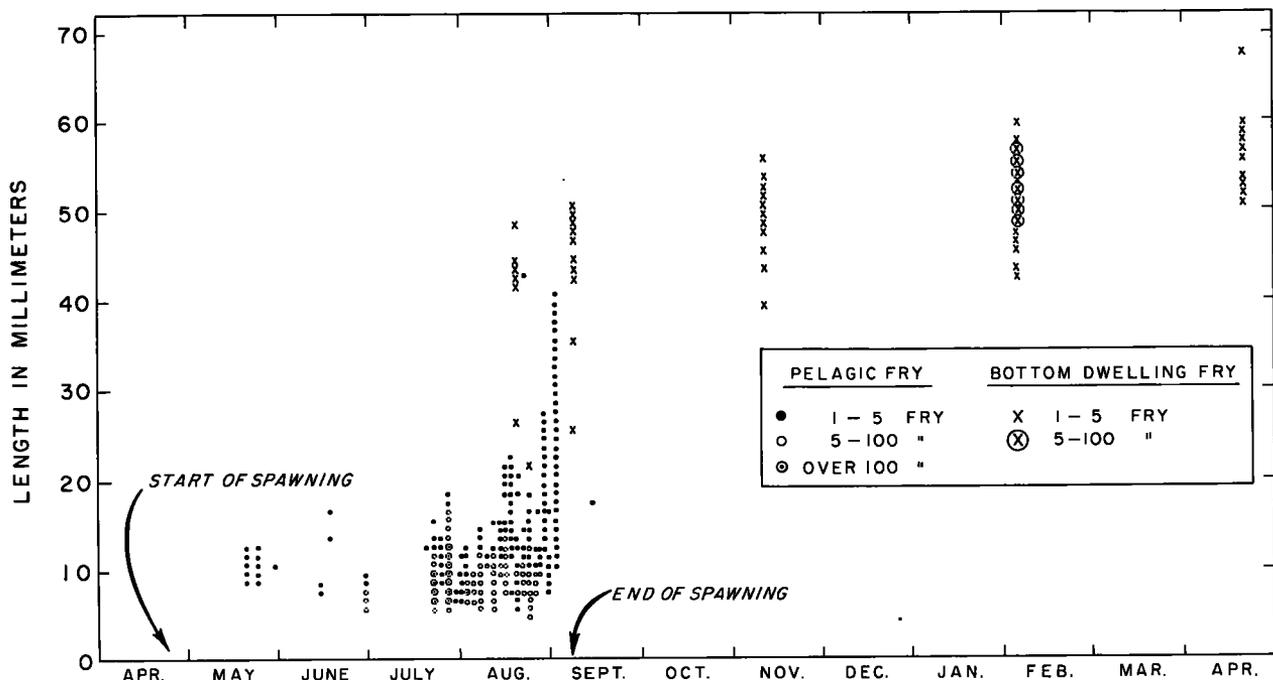


FIGURE 6.—Length frequencies of young redfish taken by research vessels in the Gulf of Maine. Data of tables 4-11 plotted by time of collection.

LENGTH COMPOSITION OF SMALLER FISH

The length composition and growth of age-groups I, II, and III (1954) taken at the New Scantum station over an 18-month period is presented in figure 7. Similar data for the first seven age groups are given in table 12. While growth in the second and third years is not as rapid as in the first year, one can clearly observe the progression of modes. It may be noted that most of the growth takes place in the period April to August. Even at these young ages there is a wide range of sizes in any one age group.

TABLE 4.—Length frequencies of 781 redfish fry from the R/V Grampus collections in the Gulf of Maine, 1912 [Data from Bigelow 1914]

Length	July			August							
	22	24	29	7	14	15	16	22	24	29	31
5 mm				16							
6 mm		3	67	28							
7 mm		2	212	39	8	1	7	7			1
8 mm			34	37	16	3	10	6			1
9 mm			4	69	28	6	7	3	1	3	2
10 mm				23	30	4	3	1	1		1
11 mm		1		14	30		2		1	1	1
12 mm	1			5	10	2		1	1		
13 mm				2	10						
14 mm				1	4		1				
15 mm					4						
16 mm									1	1	
17 mm											
18 mm					1						
19 mm					4						
20 mm					1						
21 mm					1						
Total	1	6	307	234	153	16	30	18	5	5	6

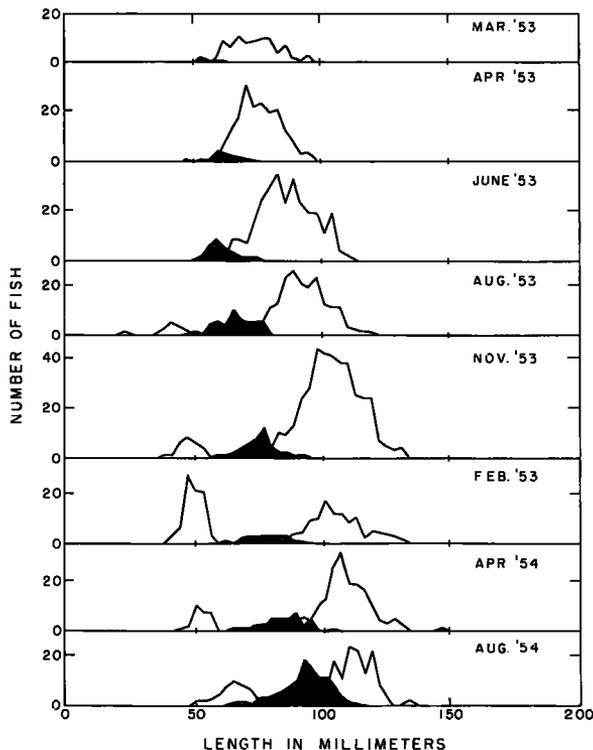


FIGURE 7.—Length composition of the three youngest age groups collected at the New Scantum station in 1953 (<I, I, and II) and 1954 (I, II, and III). The 1952 year class is shaded.

TABLE 5.—Length frequencies of 457 redfish fry from the R/V Grampus collections in the Gulf of Maine, 1914

[Data from Bigelow 1917; exact count of specimens not available]

Length	July				August						
	24	25	27	28	11	12	13				
5 mm											
6 mm				X							
7 mm				X				X			
8 mm	X	X		X							
9 mm	X	X	X	X	X			X	X		
10 mm	X	X	X	X	X	X		X	X		
11 mm	X	X	X	X	X	X		X	X		
12 mm	X		X	X	X	X		X	X		
13 mm	X				X	X		X	X		
14 mm					X	X		X	X		
15 mm					X	X		X	X		
16 mm						X		X	X		
17 mm						X		X	X		
18 mm						X		X	X		
19 mm						X		X	X		
20 mm						X		X	X		
21 mm						X		X	X		
22 mm						X		X	X		
23 mm						X		X	X		
Total	6	38	42	43	150	2	104	21	1	35	15

TABLE 6.—Length frequencies of redfish fry from the R/V Grampus collections in the Gulf of Maine, 1915

[Data from Bigelow 1917; some material still available was measured and data included; exact count of specimens not available]

Length	May 31	June 14	August			September			Station 10300			
			4	6-7 ¹	31	1	2	14				
5 mm												
6 mm			X									
7 mm		X	X									
8 mm		X	X						1			
9 mm		X	X	1					2			
10 mm	X						X					
11 mm				1			X					
12 mm					X		X	2				
13 mm					X		X					
14 mm					X		X	1				
15 mm					X		X	1				
16 mm					X		X					
17 mm					X		X		1			
18 mm					X		X					
19 mm					X		X					
20 mm					X		X					
21 mm					X		X					
22 mm					X		X					
23 mm					X		X					
24 mm					X		X					
25 mm					X		X					
26 mm					X		X					
27 mm					X		X					
28 mm					X		X					
29 mm					X		X					
30 mm					X		X					
31 mm					X		X					
32 mm					X		X					
33 mm					X		X					
34 mm					X		X					
35 mm					X		X					
36 mm					X		X					
37 mm					X		X					
38 mm					X		X					
39 mm					X		X					
40 mm					X		X					
Total	1	2	Many	2	20	24	Swarm	1	3	4	1	3

¹ Specimens found among old collections and larvae were measured.

TABLE 7.—Length frequencies of 97 redfish fry from the R/V Albatross II collections in the Gulf of Maine, 1931

[Measurements made from preserved material]

Length	May		June		Between June 18 and July 10
	21	22	17	18	
5 mm					12
6 mm					52
7 mm					15
8 mm	1	1			1
9 mm	2	1			2
10 mm	2	2			
11 mm	1	1			
12 mm	1	1			
13 mm			1		
16 mm				1	
17 mm					
Total	7	6	1	1	82

TABLE 8.—Length frequencies of 2,234 redfish fry from the R/V Atlantis collections in the Gulf of Maine, 1932

[Measurements of preserved material]

Length	July		
	22	23	24
5 mm	11	75	42
6 mm	15	235	111
7 mm	11	264	147
8 mm	7	189	176
9 mm	3	96	221
10 mm	1	49	201
11 mm		12	173
12 mm		2	99
13 mm		1	44
14 mm			26
15 mm		1	13
16 mm			6
17 mm			2
18 mm			1
Total	48	924	1,282

TABLE 9.—Length frequencies of 53 redfish fry from the R/V Albatross III and M/V Priscilla V collections in the Gulf of Maine, 1953

[Measurements of preserved material]

Length	August 17	September 8	November 10
25 mm		1	
26 mm	1		
27 mm			
28 mm			
29 mm			
30 mm			
31 mm			
32 mm			
33 mm			
34 mm			
35 mm		1	
36 mm			
37 mm			
38 mm			1
39 mm			
40 mm			
41 mm	2		
42 mm	1	2	
43 mm	2	3	1
44 mm	2	3	
45 mm			2
46 mm		2	
47 mm		2	4
48 mm	2	1	2
49 mm		1	3
50 mm		1	3
51 mm			1
52 mm			2
53 mm			3
54 mm			
55 mm			4
Total	10	17	26

TABLE 10.—Length frequencies of 325 redfish fry from the M/V Priscilla V collections in the Gulf of Maine, 1954

[Measurements of preserved material]

Length	[Measurements of preserved material]		
	February 6	April 21	August 7
5 mm.....			36
6 mm.....			53
7 mm.....			59
8 mm.....			31
9 mm.....			15
10 mm.....			11
11 mm.....			7
12 mm.....			3
15 mm.....			1
42 mm.....	1		
43 mm.....	2		
45 mm.....	1		
46 mm.....	2		
47 mm.....	4		
48 mm.....	6		
49 mm.....	6		
50 mm.....	16	1	
51 mm.....	8	3	
52 mm.....	10	3	
53 mm.....	3	4	
54 mm.....	8		
55 mm.....	8	3	
56 mm.....	5	4	
57 mm.....	1	3	
58 mm.....		2	
59 mm.....	2	2	
67 mm.....		1	
Total.....	83	26	216

TABLE 11.—Length frequencies of 97 redfish fry from the R/V Albatross III collections in the Gulf of Maine, 1955

[Measurements of preserved material]

Length	August		
	17	18	19
4 mm.....		3	
5 mm.....	1	13	
6 mm.....	2	10	
7 mm.....	5	7	
8 mm.....	3	5	
9 mm.....	6	8	
10 mm.....	1	4	
11 mm.....		3	
12 mm.....	2	8	
13 mm.....	1	3	
14 mm.....		4	
15 mm.....		1	
16 mm.....		2	
17 mm.....			
18 mm.....	1	1	
19 mm.....			
20 mm.....	1		
21 mm.....			1
42 mm.....			1
Total.....	23	72	2

TABLE 12.—Length frequencies of redfish, by age

Length	Age-group <I					Age-group I					Age-group II					Age-group III				
	Mar.	Apr.	June	Aug.	Nov.	Mar.	Apr.	June	Aug.	Nov.	Mar.	Apr.	June	Aug.	Nov.	Mar.	Apr.	June	Aug.	Nov.
MALES																				
40 mm.				2																
45 mm.				1	5		1													
50 mm.					5				1											
55 mm.					2		1		3											
60 mm.							5		1											
65 mm.									3											
70 mm.									7	2	3									
75 mm.									3	5	6									
80 mm.									5	7	5									
85 mm.										1	6									
90 mm.																				
95 mm.											2									
100 mm.												3								
105 mm.												6	4							
110 mm.												24	4	1						
115 mm.												4	3	8						
120 mm.												13	7	4						
125 mm.												23	13	7						
130 mm.												8	14	18		1				
135 mm.												14	21	16						
140 mm.												8	14	21						
145 mm.												10	18	27						
150 mm.												3	10	18						
155 mm.													10	15		1				
160 mm.													3	4			1			
165 mm.													2	2						1
170 mm.																				
175 mm.																				
180 mm.																				
185 mm.																				
190 mm.																				
195 mm.																				
200 mm.																				
205 mm.																				
210 mm.																				
215 mm.																				
220 mm.																				
225 mm.																				
230 mm.																				
235 mm.																				
240 mm.																				
245 mm.																				
250 mm.																				
255 mm.																				
260 mm.																				
265 mm.																				
270 mm.																				
Total males.				3	12	1	7	14	20	18	27	92	87	89	192	5	3	1		7
Average length (mm.)				44.2	51.3	57.5	59.6	62.1	68.8	75.3	79.9	79.6	88.6	93.8	106.1	103.5	105.8	122.5		134.6

TABLE 12.—Length frequencies of redfish, by age

Length	Age-group <I					Age-group I					Age-group II					Age-group III					
	Mar.	Apr.	June	Aug.	Nov.	Mar.	Apr.	June	Aug.	Nov.	Mar.	Apr.	June	Aug.	Nov.	Mar.	Apr.	June	Aug.	Nov.	
FEMALES																					
25 mm				1																	
30 mm																					
35 mm					1																
40 mm				3	1																
45 mm					6																
50 mm					4			1													
55 mm					2			2	3												
60 mm						1		2	4	1	3	1									
65 mm								4	7	3	1	10	2		1						
70 mm							1		5	2	4	23	4								
75 mm									4	8	5	21	4	3							
80 mm									1	10	4	15	6	7				1			
85 mm										3	1	13	10	17							
90 mm										2	1	2	9	18				1			
95 mm												1	6	19				1	1		
100 mm													6	11				2	2		
105 mm													2	14				1		1	1
110 mm													1	4						2	
115 mm														1							1
120 mm														1				1			1
125 mm																					1
130 mm																					1
135 mm																					1
140 mm																					2
145 mm																					1
150 mm																					
155 mm																					
160 mm																					
165 mm																					1
170 mm																					
175 mm																					
180 mm																					
185 mm																					
190 mm																					
195 mm																					
200 mm																					
205 mm																					
210 mm																					
215 mm																					
220 mm																					
225 mm																					
230 mm																					
235 mm																					
240 mm																					
245 mm																					
250 mm																					
255 mm																					
260 mm																					
265 mm																					
Total females				4	14		4	5	24	29	19	87	50	95	197	5	6	4	2	9	
Average length (mm.)				38.8	49.3		63.8	58.5	68.8	79.4	75.9	77.6	83.1	96.2	106.0	106.5	100.0	116.3	112.0	136.4	
Grand total				7	26	1	11	19	44	47	46	179	137	184	389	10	9	5	2	16	
Grand average length (mm.)				41.1	50.2	57.5	61.1	61.2	68.8	77.8	78.2	78.6	80.2	95.0	106.0	105.0	101.9	117.5	112.0	135.6	

LENGTH COMPOSITION OF AGE GROUPS

The length composition of 18 age groups (<1 to XVII) by sex is presented in figure 8 and in table 13. It may be noted again how large a size range there is within any one age group. In the tenth

year, when most of the redfish have become mature, the growth rates of the males and females change, the females continuing at the higher rate. This difference becomes quite distinct within a period of only 1 year.

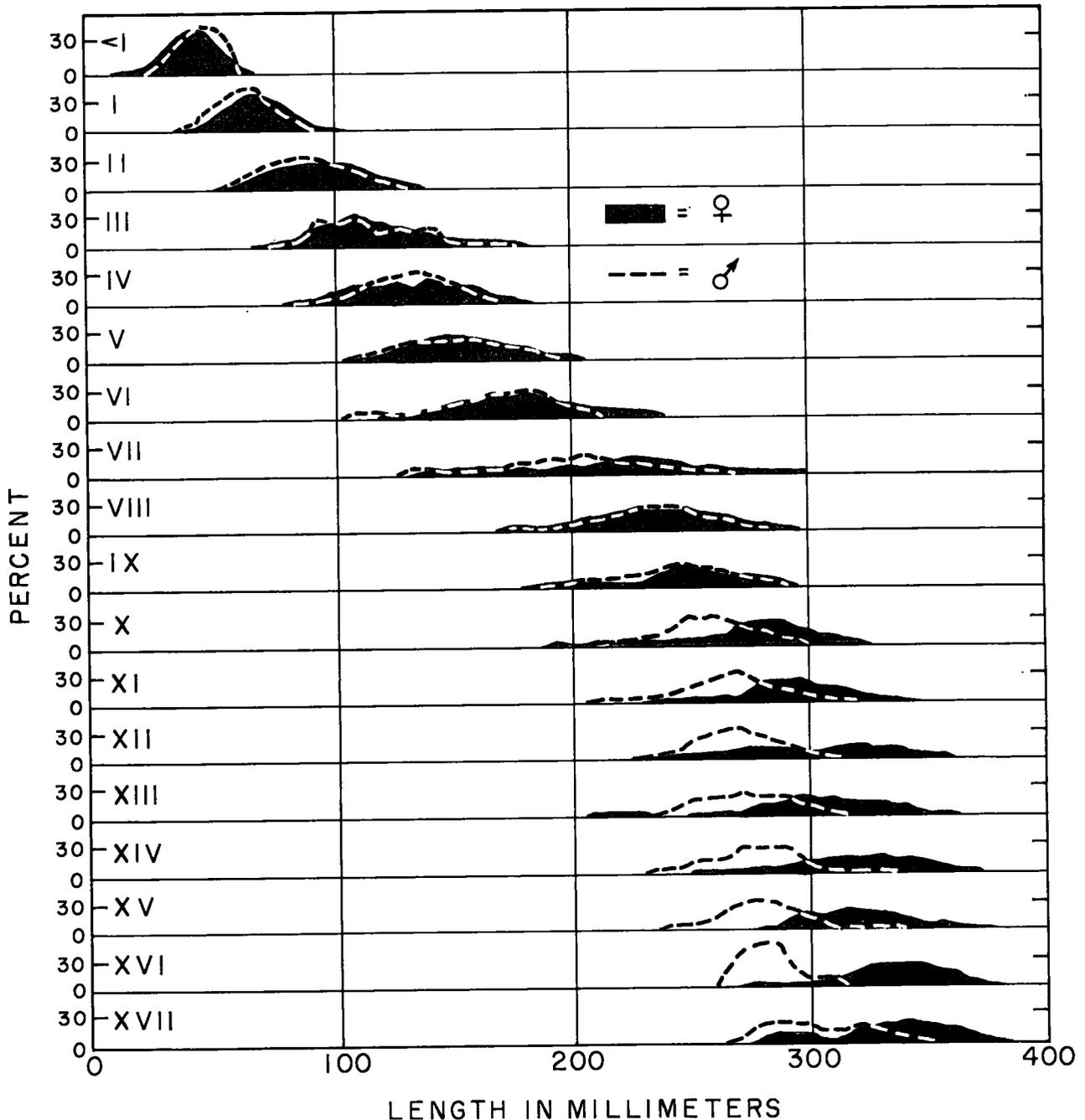


FIGURE 8.—Length composition of all age groups in combined samples of redfish taken in the Gulf of Maine in 1953 by research vessels and the commercial fishery, totaling 1,255 males and 1,251 females. (5-mm. groups smoothed by moving average of 5.)

GROWTH RATE

Growth curves for the redfish, sexes treated separately and combined, are presented in figure 9. The mean lengths at age for the sexes separately and combined are listed in tables 14 and 15. Males and females grow at approximately the same rate for the first 10 years of life. The growth curve is unusual in that for the first 10 years it is approxi-

mately linear. At 20 years of age, the growth rate of both the male and the female has markedly decreased, but it is apparent the fish are still making definite growth. Growth curves (fig. 10) in the years 1951, 1952, and 1953 are generally alike but there are some slight differences. Whether these are significant cannot be stated at this time.

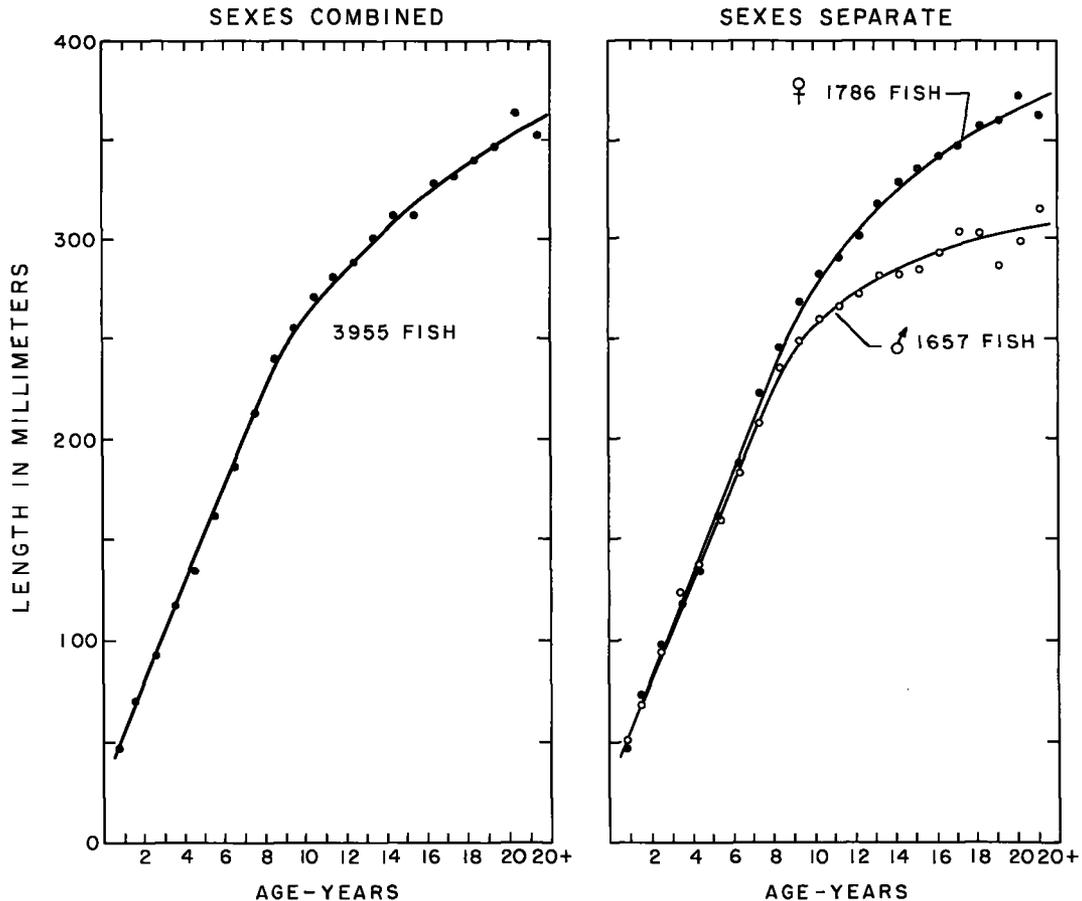


FIGURE 9.—Growth curves for the sexes, separate and combined, fitted to the mean lengths at age and based on samples of redfish from catches of the research vessels and the commercial fishery, collected in the Gulf of Maine in 1951, 1952, and 1953. The growth curve of the sexes combined includes 512 unsexed fish. (See table 14.)

TABLE 13.—Length frequencies of redfish, by age

[Based on all research-vessel and

Length	Number of males in age-group—																					
	<I	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XX+
25 mm																						
30 mm																						
35 mm																						
40 mm	2																					
45 mm	5																					
50 mm	6																					
55 mm	1																					
60 mm	18	1																				
65 mm	11	13																				
70 mm	8	35																				
75 mm	12	40																				
80 mm	2	52																				
85 mm	1	55																				
90 mm		59																				
95 mm		60																				
100 mm		59																				
105 mm		36																				
110 mm		39																				
115 mm		20																				
120 mm		12																				
125 mm		2																				
130 mm		4																				
135 mm																						
140 mm																						
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365 mm																						
370 mm																						
375 mm																						
380 mm																						
385 mm																						
390 mm																						
395 mm																						
400 mm																						
Total fish..	15	60	487	16	97	150	56	53	42	46	38	45	39	31	23	23	8	13	7	3	3
Mean length (mm.)	49.8	67.9	94.2	118.8	135.2	157.1	177.5	203.7	238.9	245.0	262.1	265.9	272.8	278.0	280.5	282.3	283.1	306.3	293.9	279.2	312.5

TABLE 14.—Length frequencies of redfish, by age group, sexes combined, from all samples collected in the Gulf of Maine in 1951, 1952, and 1953

[Includes 512 unsexed fish]

Length	Number of fish (sexes combined) in age-group—																					
	<I	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XX+
25 mm.	2																					
30 mm.																						
35 mm.	2																					
40 mm.	15																					
45 mm.	19	1																				
50 mm.	11	3																				
55 mm.	4	15	1																			
60 mm.		31	9																			
65 mm.		22	38																			
70 mm.		19	81	1																		
75 mm.		25	97	1																		
80 mm.		13	123	2																		
85 mm.		4	135	1	1																	
90 mm.		2	136	1	2																	
95 mm.			130	8	4																	
100 mm.			114	11	3																	
105 mm.			106	15	12																	
110 mm.			72	9	17	1																
115 mm.			39	7	16	3																
120 mm.			32	6	23	11	2															
125 mm.			6	7	19	10	2															
130 mm.			6	3	20	17	2															
135 mm.			6	3	26	23	2	1														
140 mm.			3	3	22	21	3		1													
145 mm.			4	2	23	37	7	3														
150 mm.			2	2	28	31	6	3														
155 mm.			1	1	12	36	7	3		2												
160 mm.					5	31	4	4	1													
165 mm.				1	7	34	12	4	1													
170 mm.					1	25	13	6	3													
175 mm.					1	28	15	5				1										
180 mm.					2	13	25	8				1										
185 mm.						16	17	9	6			1										
190 mm.			1			13	22	10	2	2												
195 mm.						2	19	17	3	3		1										
200 mm.					1	8	22	23	4	2		1		1								
205 mm.					1	11	13	8	3	7		3		1								
210 mm.						7	13	4	3	1		1		1								
215 mm.						11	12	8	6	6		1										
220 mm.						5	12	8	2	4		1			1							
225 mm.						1	3	10	12	3		4										
230 mm.						2	9	9	9	5		1		1								
235 mm.						1	8	16	6	3		4		2								
240 mm.						10	21	15	3	3		6		3								
245 mm.						2	4	8	14	7		3		3								
250 mm.						9	17	14	14	9		9		4		1						
255 mm.						1	6	10	17	10		7		10		5						
260 mm.						6	1	13	6	21		12		11		6		1		1		
265 mm.						3	6	13	6	13		12		6		3		1				
270 mm.						10	6	10	13	14		13		11		7		1				
275 mm.						5	5	13	7	11		9		10		7		5		2		
280 mm.						6	16	14	15	10		10		10		10		5		3		
285 mm.						2	7	13	15	14		10		4		4		6		2		
290 mm.						1	6	12	10	10		4		10		6		4		4		1
295 mm.						2	3	5	8	9		7		5		5		8		2		
300 mm.						3	2	6	5	5		8		10		5		5		2		1
305 mm.						1	2	6	8	8		11		5		3		3				
310 mm.						2	1	5	10	7		9		6		1		5		2		1
315 mm.								3	3	3		11		6		9		6		2		
320 mm.								2	3	6		5		7		6		2		2		1
325 mm.								1	1	1		3		7		7		3		1		1
330 mm.								3	1	5		4		2		2		4		2		1
335 mm.								1				3		5		5		2		4		2
340 mm.										1		2		4		9		5		6		2
345 mm.												4		1		9		3		4		1
350 mm.										1		5		5		5		2		5		1
355 mm.												1		1		2		4		2		1
360 mm.												2		2		7		5		4		2
365 mm.												1		1		7		3		1		1
370 mm.														1		3		1		3		2
375 mm.														1		1		1		2		1
380 mm.												1								1		
385 mm.																				3		
390 mm.																				1		1
395 mm.																				1		
400 mm.																						1
405 mm.																						
Total fish.	53	135	1,125	90	246	369	231	217	187	180	175	170	179	145	133	89	71	67	38	28	10	17
Mean length (mm.)	46.7	69.7	93.3	112.1	135.4	160.5	185.9	213.0	240.3	254.8	269.8	280.1	287.7	300.0	310.9	310.6	323.6	331.4	339.7	347.3	367.5	351.3

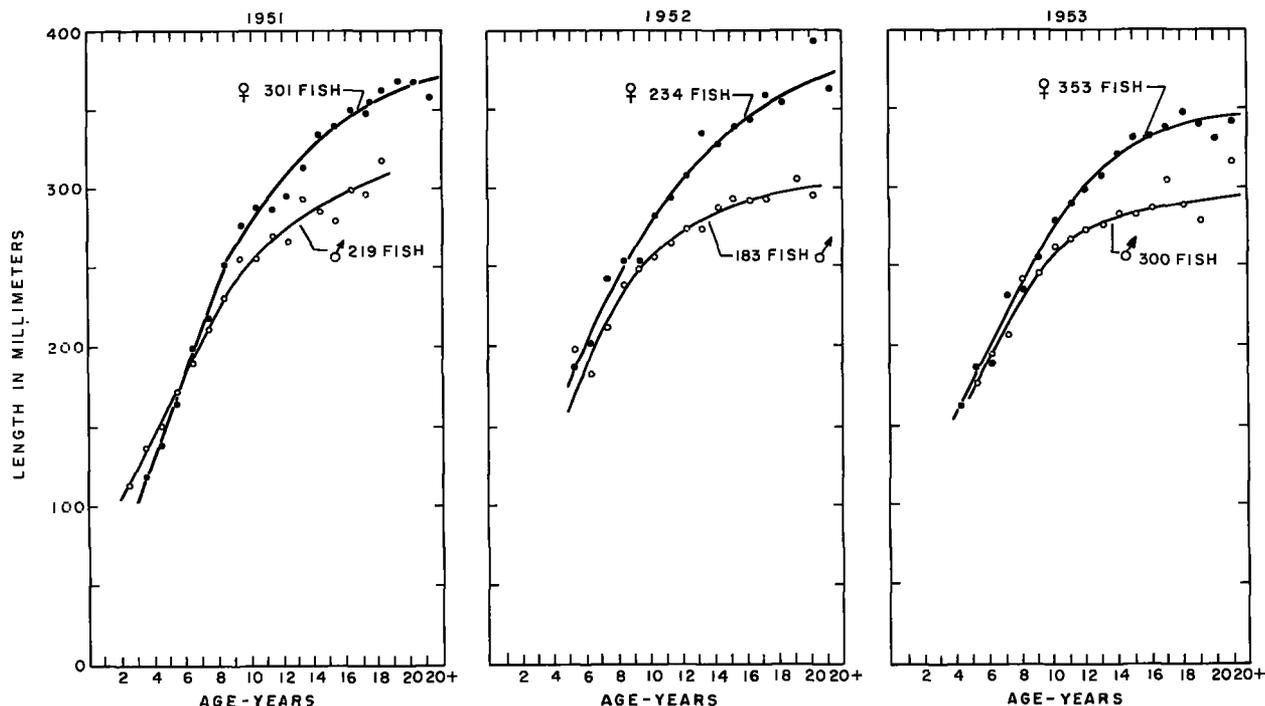


FIGURE 10.—Growth curves for the sexes fitted to the mean lengths at age, for redfish sampled from the commercial fishery in 1951, 1952, and 1953.

AGE COMPOSITION

Age composition of the redfish sampled from the commercial catch in the Gulf of Maine in 1951, 1952, and 1953 is presented in figure 11. These fish ranged in age from 2 to more than 20 years. The bulk of the fish were from 6 to 14 years of age. Certainly in these samples there is no striking evidence of excessive reduction of the older age groups from one year to the next. It is interesting, therefore, to observe the data presented in figure 12 on the changes in length composition of samples that are available for the period 1936 to 1953. The most obvious change is the decrease in the modal groups over the length range of 27 to 32 cm. These are fish of approximately 10 to 15 years of age.

There are possible explanations for the changes observed over this 18-year period. The modes which appear in 1936 dominated the fishery and may very well represent one or more very strong year classes. This could account for the relatively greater number of older fish some years later. There is a detectable shift toward the smaller sizes from 1941 on. In the period 1945 to 1949 there appears to have been another strong year class; the mode moves from about 25 cm. in 1945 to 28 cm. in 1949. Again in 1949, another such group is suggested at around 25 cm., reaching 27 to 28 cm. by 1953. This argument is admittedly tenuous; however, the data do suggest that there may well have been some very strong year classes during the period 1936 to 1953, and since 1936, at least, the biggest fish have not been excessively exploited in proportion to the smaller size groups.

TABLE 15.—Length frequencies of redfish, by sex and age group, from

Length	Number of males in age-group—																					
	<I	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XX+
25 mm.																						
30 mm.																						
35 mm.																						
40 mm.	2																					
45 mm.	6	1																				
50 mm.	5	1																				
55 mm.	2	6																				
60 mm.	18	1																				
65 mm.	11	13																				
70 mm.	8	35																				
75 mm.	12	40																				
80 mm.	2	52																				
85 mm.	1	55	1																			
90 mm.		59		1																		
95 mm.		60		2																		
100 mm.		59	2	1																		
105 mm.		36	5	2																		
110 mm.		40	1				1															
115 mm.		20	6	8	1																	
120 mm.		12	2	11	7	1																
125 mm.		2	2	5	8	1																
130 mm.		4	1	9	9	2																
135 mm.		3	13	10	7		1															
140 mm.		1	11	10	4	1		2														
145 mm.		1	19	17	4																	
150 mm.			2	9	14	1																
155 mm.				14	4	2				2												
160 mm.				1	20	5	1															
165 mm.				4	17	7	3		1													
170 mm.					8	3	3		3													
175 mm.				1	17	7					1											
180 mm.					7	15	5		1													
185 mm.					6	8	4		5													
190 mm.					6	10	4		1	1												
195 mm.					1	12	9		1		1											
200 mm.					1	7	10		2													
205 mm.					1	4	7		1	3	1											
210 mm.						2	6		2	2	1											
215 mm.						5	5		3	4												
220 mm.						1	5		3	2	3	1										
225 mm.							4		4	2	2											
230 mm.						2	6		4	5	3	1	1									
235 mm.							2		11	6	2											
240 mm.							4		12	7	3	5	1	1								
245 mm.							1	2	4	8	4	2	3		1							
250 mm.								4	5	8	10	4	8	3	1					1		
255 mm.							1	4	4	10	9	4	5	1	1							
260 mm.								4	3	8	13	8	10	5	5	5						
265 mm.								1	3	8	5	11	7	3	2	3	1			1		
270 mm.									2	5	5	11	9	9	4	1						
275 mm.									2	7	4	4	7	6	4	5	1					
280 mm.									2	2	3	8	10	7	8	5			3		2	
285 mm.										2	5	3	5	4	4	4			3		1	
290 mm.									1	2	3	3	6	2	2	4			2			1
295 mm.									1		3	3	1	6	3	7			2			
300 mm.											1	1	1	1	1	2				1		1
305 mm.																			3			
310 mm.												1							2			1
315 mm.																			1			
320 mm.																			1			1
325 mm.															1							
330 mm.															1	1						
335 mm.																			2			
340 mm.																			1			
345 mm.																				1		
350 mm.																			1			
355 mm.																						
360 mm.																						
365 mm.																						
370 mm.																						
375 mm.																						
380 mm.																						
385 mm.																						
390 mm.																						
395 mm.																						
400 mm.																						
405 mm.																						
430 mm.																						
Total fish..	15	60	488	21	113	176	101	92	82	90	78	73	76	55	38	38	23	20	10	4	1	3
Mean length (mm.)	49.8	67.9	94.3	122.7	137.3	160.2	183.1	206.8	235.4	248.2	258.6	266.0	270.9	279.8	281.1	283.2	291.4	301.5	301.0	285.0	292.5	312.5

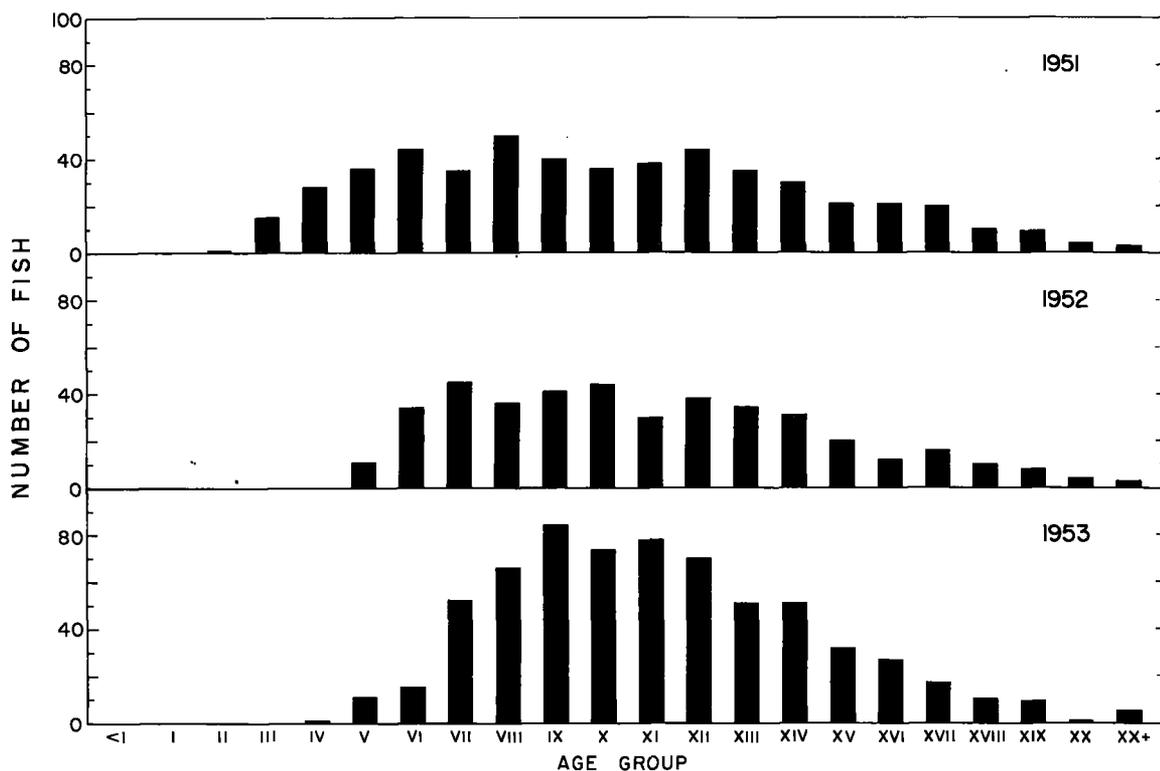


FIGURE 11.—Age composition of redfish sampled from the commercial catch in the Gulf of Maine, 1951, 1952, and 1953.

Age composition of the juvenile fish taken from the New Scantum station off Cape Ann shows large differences in year-class strength (fig. 13). These fish ranged in age from young of the year to 7-year-olds. Age-groups II and V stand out in the 1953 collections. Age-groups III and IV were notably lacking. The same age-group relation existed in the 1954 collections. The age-group data presented in figures 11 and 13 suggest that these age-group differences lessened by the time the fish became available to the commercial fishery.

DISCUSSION AND CONCLUSIONS

Our data show that only one annulus is formed per year in the otolith of the redfish of the western Atlantic. This conclusion is in accord with that of Bratberg (1956) for the redfish of the eastern Atlantic.

There is no doubt in our minds that redfish lay down only one annulus a year. While it is understandable how incorrect interpretations of length-frequency data are possible when one considers the exceptionally wide spread of sizes at age, there is no justification for suggesting that more than one annulus is laid down each year in

the otoliths, on the basis of subjective analysis of redfish length-frequency data. Some other form of verification must be submitted before any consideration can be given to the suggestion that more than one opaque and one hyaline band is laid down in a single year in the otolith.

It is our opinion that the young do not normally pass through the winter scaleless and that an annulus is formed in both scale and otolith during the first winter. However, the time of first-annulus formation in the scales could be markedly affected by several factors. Hydrographic conditions vary greatly within the Gulf of Maine. The initial growth of the young redfish may not be sufficient in areas farther north, around Greenland for example, for them to start scales before the first winter. The time at which the larvae are spawned likewise could profoundly affect the growth attained in the first year.

Bratberg established the concomitance of annulus formation in scale and otolith. To detect annulus formation, there must be sufficient new growth to contrast with the old. Bratberg studied changes in the spacing of the circuli in the scale and the seasonal accretion of opaque material

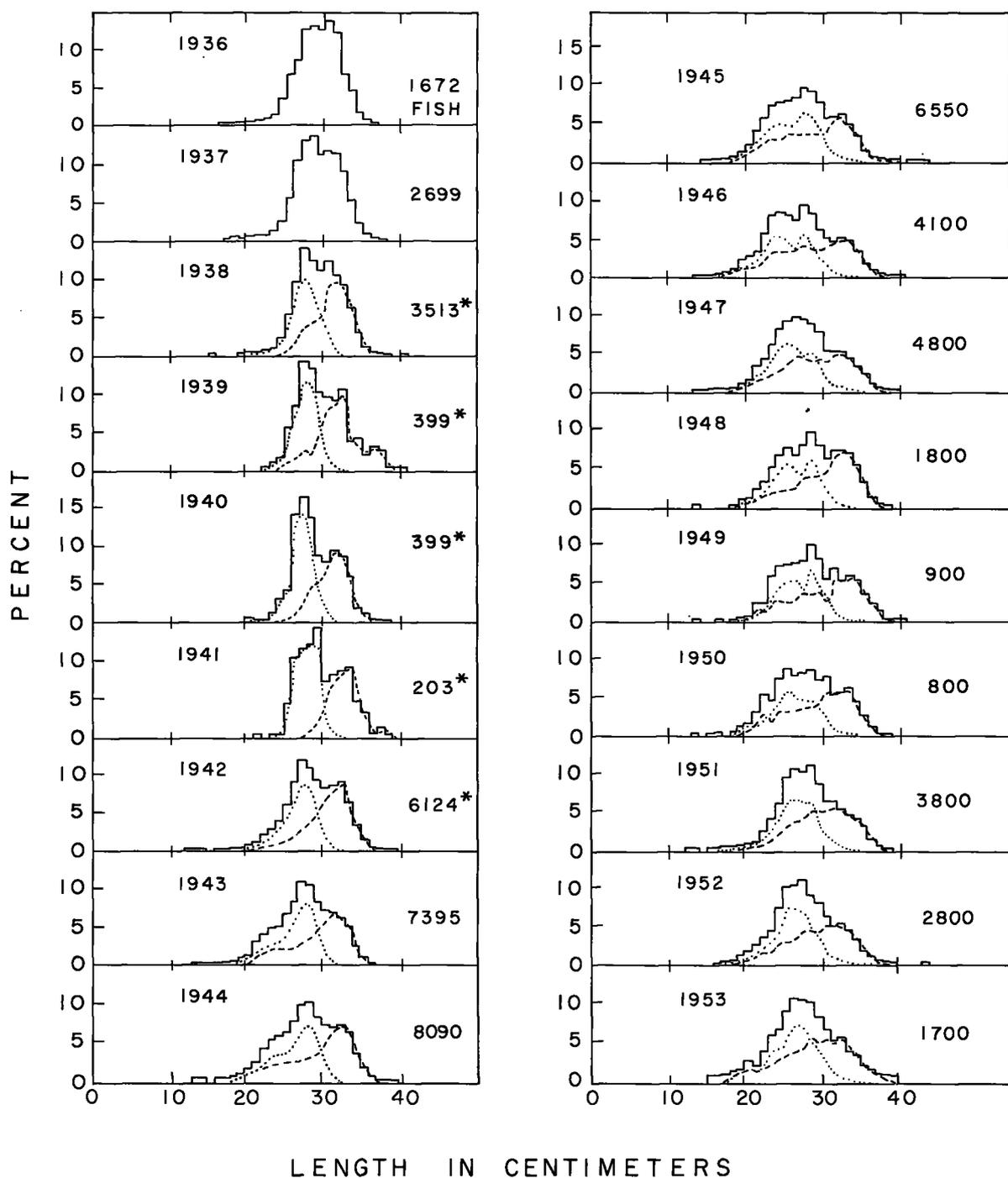


FIGURE 12.—Percentage length composition of redfish, by sex, sampled from the commercial catch in the Gulf of Maine, 1936 to 1953. No data are available on distribution of the sexes for 1936 and 1937; and only a portion of the sample was sexed for the years 1938 through 1942, as indicated by an asterisk (*). Females (dashed line); males (dotted line).

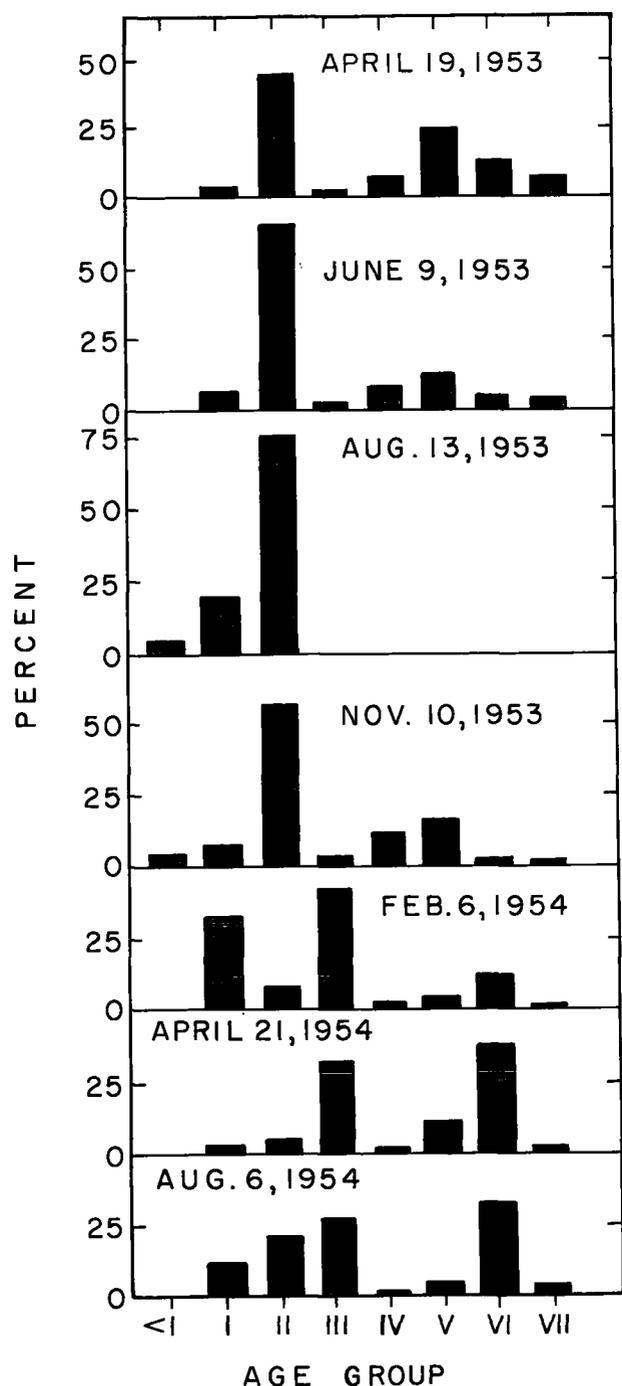


FIGURE 13.—Percentage age composition of redfish, pre-annulus to age-group VII, collected at New Scantum station, April 1953 to August 1954.

in the otolith. His study indicated that the annulus in both the scale and the otolith began to form in March and April. By May all fish showed obvious signs of new growth. Similarly, the

studies reported in this paper show a sharp increase in April in the percentage of otoliths with an opaque edge, with over 90 percent of the otoliths having an obvious annulus by the early part of June. Another study—that of Perlmutter and Clarke—showed essentially the same thing. Their data suggested quite strongly that renewed growth may be detected on the scales in April. Further, the greatest number of scales with narrowly spaced circuli were taken from fish collected in February. All of these findings are consistent.

The age-composition studies of small fish provided verification of our interpretation of the otolith. In figure 13, it is apparent that there were two dominant year classes in the samples taken off Cape Ann. This population was followed for a period of 18 months, during which the complete cycle of the banding of the otolith was studied. When the fish were first collected in April 1953, the otoliths were observed to be developing the opaque band. By February 1954, the otoliths uniformly bore hyaline bands. The opaque bands were beginning to develop again in April, and by August all had well-developed opaque bands. It is plain that the sequence observed of year-class dominance could not have occurred had the otoliths laid down several series of bands. If they had, the dominant year classes would have appeared to have aged several years during the 18-month period of sampling.

The wide differences in length at age observed may be the result of the failure of some young fish to form a discernible annulus the first year. More likely, it is a result of the extended period of spawning. Collections made in late summer contain young redfish varying in length from 10 mm. to more than 50 mm. For this reason, even assuming that all these redfish put down a detectable annulus during their first winter, it is not surprising to find that any one age group taken from the commercial catch may have a length range of more than 100 mm. It is not necessary to hypothesize extremes in growth rates to account for the spread of sizes at age.

Most of our data on the length at age is based on samples of the commercial catch, and these samples come from many areas in the Gulf of Maine. Most biologists working with redfish believe that the fish move about very little and this admits the possibility of different growth rates in different areas.

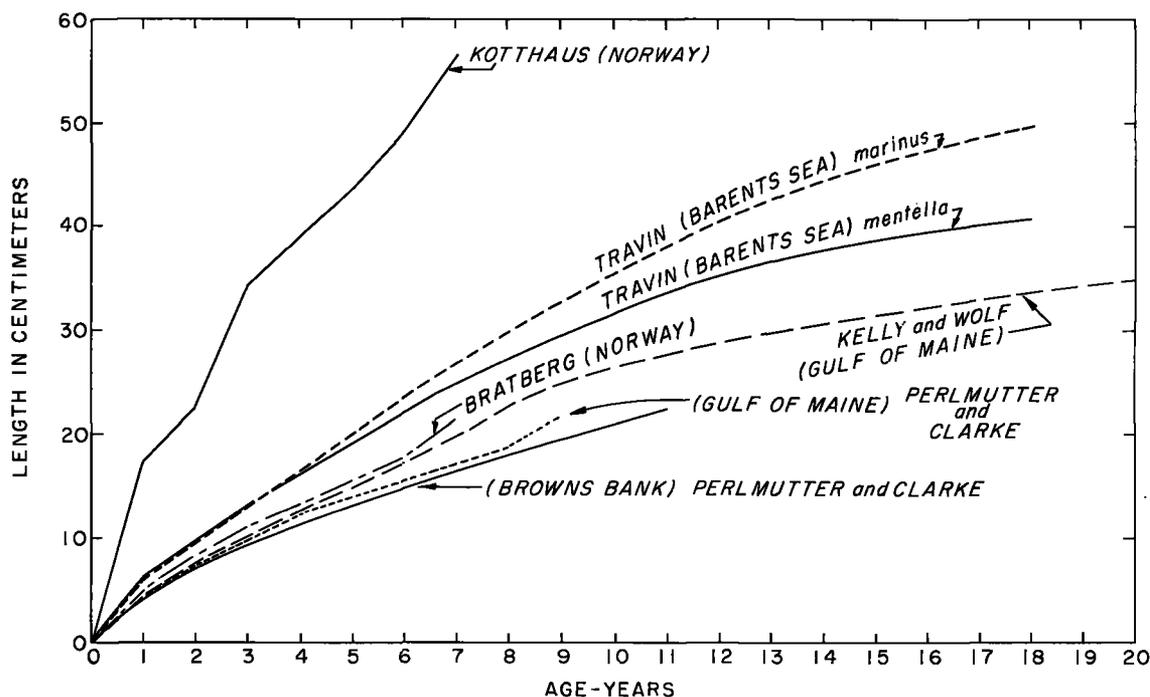


FIGURE 14.—Comparative growth rates of various *Sebastes* populations.

All important and relevant growth data that have been published to date are presented in table 16. All growth data based on the premise of a single annulus a year are consistent. The data of table 16, with the exception of those of Smaragdova and Veschezzerov, are presented in figure 14 in the form of growth curves for the purpose of comparison. The erratic nature of Smaragdova's data (the age appears to be underestimated occasionally) was probably due to the fact that he used a geographically mixed sample. To a lesser degree, the same remarks possibly apply to Veschezzerov's data. It must be remembered that until Travin published his paper there were at least two fairly well-defined population groups that were not recognized as such in the northern European waters. Travin's age-growth data for the subspecies *marinus* and *mentella* from the Barents Sea show the rate of growth of the populations. A growth rate derived from Bratberg's data is virtually identical to the growth rate for redfish from the Gulf of Maine. Perlmutter and Clarke's growth data on the Browns Bank redfish show the slowest growth of any group of redfish. The curve based on their Gulf of Maine material adjusted for time

of annulus formation indicates a somewhat slower rate of growth than we found. The age-length data presented by Kotthaus are also plotted to show the extreme differences between his concept of redfish growth and that of other workers.

Kotthaus (1952) reported fish longer than 80 cm. from European waters. In recent years, several specimens measuring between 74 and 83 cm. in length and weighing from 14½ to 19½ pounds have been landed at Gloucester, and some have been reported in the local newspaper (Gloucester Times, July 30, 1953, and April 5, 1955). Most of these large fish came from the southeastern Grand Bank. It is interesting to speculate on the possible age of such fish. Our data indicate that it would be possible for one of the faster-growing females to reach this size in about 40 to 50 years. It seems probable that some redfish may live to an age in excess of even 50 years.

In conclusion, our results agree with those of several of the earlier growth studies and especially with those which were based on the premise of one annulus being laid down each year. It is evident that *Sebastes* is a slow-growing, long-lived fish.

TABLE 16.—Growth studies of the redfish, *Sebastes marinus marinus* and *S. m. mentella*, in the North Atlantic Ocean

[Age in years; average length in cm., on January 1]

Age	Average length of—								<i>Sebastes marinus mentella</i>	
	<i>Sebastes marinus marinus</i>									
	Barents Sea			Browns Bank	Gulf of Maine		Norway	Norway coast		Barents Sea
	Smaragdova (1936)	Veschezerov (1944)	Travin (1951)	Perlmutter and Clarke ¹ (1949)	Perlmutter and Clarke ¹ (1949)	Kelly and Wolf ²	Kotthaus (1953)	Bratberg (1956)		Travin (1951)
1	5.4	5.12	6.26	4.7	5.2	5.5	17.2	5.6	6.28	
2	9.7	7.22	9.05	6.9	7.6	7.8	22.2	8.4	10.01	
3	10.0	9.06	12.87	9.2	9.9	10.1	34.2	11.3	13.09	
4	12.6	12.60	16.50	11.2	12.1	12.5	39.1	13.1	16.30	
5	14.7	15.38	19.95	13.2	13.9	14.7	43.8	15.75	19.32	
6	17.4	18.20	23.49	15.0	15.4	17.3	49.0	17.95	22.10	
7	17.5	21.30	26.61	16.7	16.9	19.8	56.6	21.45	25.27	
8	20.1	24.60	29.62	18.1	18.9	22.7			27.77	
9	19.6	28.06	32.69	19.3	21.8	24.9			29.84	
10	21.6	32.84	35.33	20.8		26.3			31.81	
11	22.5	36.68	38.00	22.5		27.4			33.44	
12	25.5	38.70	40.46			28.5			35.20	
13	28.6	40.08	42.46			29.5			36.47	
14	31.3	43.50	44.07			30.4			37.69	
15	32.3	45.28	45.82			31.3			38.51	
16	36.3	46.40	47.18			32.1			39.12	
17	39.2	48.46	48.17			32.8			40.16	
18	44.9	50.02	49.86			33.6			40.45	
19	46.8	50.62				34.4				
20	47.5	51.02				35.0				
21	51.2	53.00								
22	52.4	53.35								
23	53.9	54.33								
24	54.9	55.33								
25	55.4									
26	57.0									
27	57.0									

¹ Average length adjusted to observed annulus number.² Present study.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

**THE GOLDEYE, *AMPHIODON ALOSOIDES*
(RAFINESQUE), IN THE COMMERCIAL
FISHERY OF THE RED LAKES
MINNESOTA**

BY MARVIN D. GROSSLEIN AND LLOYD L. SMITH, JR.



FISHERY BULLETIN 157

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ABSTRACT

The goldeye, *Amphiodon alosoides* (Rafinesque), formerly an important species in the fishery of the Red Lakes, Minnesota, has been reduced in abundance during recent years. The decline has been significantly correlated with increased fishing effort but not with abundance of predaceous species. Growth rates of the sexes are similar in earlier years of life but the females grow faster in later years. Growth is positively correlated with summer temperatures and shows marked differences in different years. Fish attain maximum availability to commercial gill nets at a length of 13.0 to 13.4 inches and an age of 4 to 5 years. The commercial take is dependent on two or three age groups and annual abundance is strongly influenced by the strength of individual year classes. Management would be limited to control of fishing effort, but it cannot be practiced in the fishery unless entrapment gear is used instead of gill nets.

THE GOLDEYE, *AMPHIODON ALOSOIDES* (RAFINESQUE), IN THE COMMERCIAL FISHERY OF THE RED LAKES, MINNESOTA

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The commercial fishery of the Red Lakes in north-central Minnesota is a major industry of the Red Lakes band of Chippewa Indians. This fishery has been in continuous operation since 1917 and at present is carried on exclusively by members of the tribe, who market their catch through the Red Lakes Fishery Association, a cooperative organization of the Indians. A discussion of production and associated trends in the commercial fishery of the Red Lakes has been presented by Smith and Krefling (1954).

In recent years, commercial fishing in the Red Lakes has been done exclusively by some 200 Indian fishermen who use 3½-inch-mesh (stretch measure) gill nets operated from skiffs powered by outboard motors. The Red Lakes are exploited primarily for the walleye, *Stizostedion v. vitreum* (Mitchill), and the yellow perch, *Perca flavescens* (Mitchill), which contribute an average of 63 percent and 20 percent of the total annual catch. The remaining 17 percent includes the goldeye, *Amphiodon alosoides* (Rafinesque), northern pike, *Esox lucius* L., whitefish, *Coregonus clupeaformis* (Mitchill), and other species.

The University of Minnesota and the United States Fish and Wildlife Service in cooperation with the Bureau of Indian Affairs and the Red Lakes Fishery Association initiated a fishery study covering all commercial species in 1949 to provide data on which to base management and to investigate population fluctuations and associated factors.

The marked decline in the production of gold-eyes from the Red Lakes in recent years has resulted in an economic loss to the fishery. This fact and the general scarcity of published information on the species led to the present study, which deals with some phases of goldeye life

history and factors influencing abundance of the species.

Samples totaling 2,821 goldeyes were taken from the commercial catches in 1949-53. In 1950, 43 goldeyes were caught by experimental gill nets. Scale samples were obtained from 1,612 fish and lengths only from the remainder. Scale impressions were made on cellulose-acetate slides by a heat-impression method (Butler and Smith, 1953) and were examined and measured on an Eberbach scale projector at 28 × magnification. Catch statistics were taken from records of the Red Lakes Fishery Association.

Robert L. Butler, Richard L. Pycha, and John Magnuson assisted in the collection of field data and in preparation of the manuscript; Dr. E. F. Cook and J. W. Barnes aided in the identification of insects; cooperation of the staff of the Red Lakes Fishery Association in the field made the study possible. Financial assistance was provided by the Great Lakes Fishery Investigations, Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service.

PRODUCTION AND ABUNDANCE

Since 1930, when detailed records of statistics of catch and fishing effort in the commercial fishery of the Red Lakes, Minnesota, were started, annual production of individual species and of all species combined has fluctuated considerably. During the period 1930-53, the average annual production of all species totaled approximately 1,079,000 pounds (table 1). In most years prior to 1946, the goldeye ranked third in total yield and for the period 1930 to 1953 it contributed an average of approximately 67,000 pounds, or 6.2 percent, to the annual average total production of the fishery.

Goldeyes were reported to have been very abundant in the early years of the commercial fishery, but there was practically no market until

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TABLE 1.—Production of all species and of goldeyes in the Red Lakes commercial fishery, 1930–53

[Production in thousands of pounds; data from Smith and Krefting, 1954]

Year	All species	Goldeye	Year	All species	Goldeye
1930.....	747	26	1943.....	1,312	117
1931.....	1,062	3	1944.....	1,470	57
1932.....	984	2	1945.....	1,451	108
1933.....	783	(¹)	1946.....	1,478	48
1934.....	867	22	1947.....	1,534	52
1935.....	721	102	1948.....	1,363	15
1936.....	757	247	1949.....	1,061	18
1937.....	1,018	97	1950.....	652	49
1938.....	1,062	95	1951.....	758	10
1939.....	948	124	1952.....	1,117	4
1940.....	1,186	148	1953.....	1,054	4
1941.....	1,219	136			
1942.....	1,285	111	Average.....	1,079	67

¹ Less than 500 pounds.

smoked goldeye was introduced in 1924. Between 1930 and 1953, the lowest yield of goldeyes was in 1933, when only 362 pounds were taken. Production increased abruptly in 1934 to more than 22,000 pounds and exceeded 100,000 pounds the following year. The maximum take for the period was 247,383 pounds in 1936.

The substantial rise in total production of all species of fish in the Red Lakes after 1940 resulted from a rise in fishing intensity caused by wartime food demands. Fishing effort increased 78 percent, from an annual average of 5,965 lifts in 1930–40 to 10,639 lifts in 1941–53

TABLE 2.—Total summer lifts and average catch per lift of walleye, yellow perch, and goldeye in the Red Lakes commercial fishery, 1930–53

[Data from Smith and Krefting, 1954]

Year	Number of lifts (5-net)	Catch per lift (in pounds)		
		Walleye	Yellow perch	Goldeye
1930.....	6,596	61.0	11.3	4.0
1931.....	5,794	90.0	13.4	.3
1932.....	3,860	110.9	33.4	.5
1933.....	5,417	90.0	32.8	.1
1934.....	6,672	66.1	23.2	3.0
1935.....	7,087	40.8	21.0	13.0
1936.....	7,842	33.8	14.5	31.4
1937.....	5,172	96.3	43.5	18.6
1938.....	4,910	117.0	41.4	19.8
1939.....	5,657	95.5	33.8	21.8
1940.....	6,614	102.0	24.0	22.2
1941.....	8,086	95.6	11.2	16.7
1942.....	12,934	72.2	12.7	8.6
1943.....	14,816	52.4	13.0	7.8
1944.....	8,454	99.4	37.1	6.6
1945.....	10,596	72.9	28.2	10.1
1946.....	11,092	72.8	26.9	4.3
1947.....	12,393	69.9	25.4	4.2
1948.....	10,083	90.9	24.8	1.5
1949.....	9,905	64.0	18.7	1.8
1950.....	12,767	30.3	5.6	3.8
1951.....	12,449	44.7	9.0	.8
1952.....	7,856	83.3	50.7	.5
1953.....	6,883	78.1	65.9	.6
Average:				
1930–40.....	5,965	82.1	26.6	12.2
1941–53.....	10,639	71.3	25.3	5.2
1930–53.....	8,497	73.0	25.9	8.4

(table 2). The greater effort produced a substantially larger catch of walleyes and yellow perch, but not of goldeyes.

Fluctuations in total annual catch of all species appear to be primarily dependent on abundance of walleyes and perch and on market demand (Smith and Krefting, 1954). These two factors determine the amount of fishing and length of season, because there is a walleye quota and market conditions become unfavorable in late summer.

Since fishing effort has not been constant, estimates of abundance of all species have been based on the catch of a standard unit of gear, which consists of 1,500 linear feet of commercial gill net (5-net) set for 1 night. The average catch of goldeyes per unit of effort for the entire period 1930–53 was 8.4 pounds and the highest and lowest takes were 31.4 pounds and 0.1 pound (table 2; fig. 1). These wide fluctuations in availability correspond in general to changes in production (table 1). Since 1940, the availability of goldeye has declined steadily except for slight rises in 1945 and 1950, which were only minor interruptions in the downward trend.¹

FACTORS ASSOCIATED WITH DECLINE OF GOLDEYE

Abundance of Associated Species

The walleye is the most important potential predator of the goldeye in the Red Lakes. The coincidence of the substantial decline in availability of the goldeye with a decrease in average availability of the walleye suggests, however, that predation by the walleye is not the major controlling influence on goldeye abundance (table 2). Since the most significant predation on goldeye would occur during the first year of life, the effects of predation would probably vary with abundance of the older walleye age groups. In recent commercial goldeye catches, age-groups III through VI were predominant.² Linear correlation analyses between walleye abundance and goldeye abundance, with successive offset intervals from 3 to 6 years, were applied to the data, but no significant relationships were apparent.

¹ Subsequent to completion of the present study, young-of-the-year goldeye were collected for the first time in shore-seine hauls during 1955 and 1956. In the 1958 commercial season total production increased suddenly to 60,070 pounds and the catch per 5-net lift increased to 4.7. The later data suggest a possible reversal of trend such as occurred in 1935.

² Age groups are given in terms of number of annuli on the scales; fish hatched in 1950 and taken in 1953 belong to age-group III throughout the calendar year.

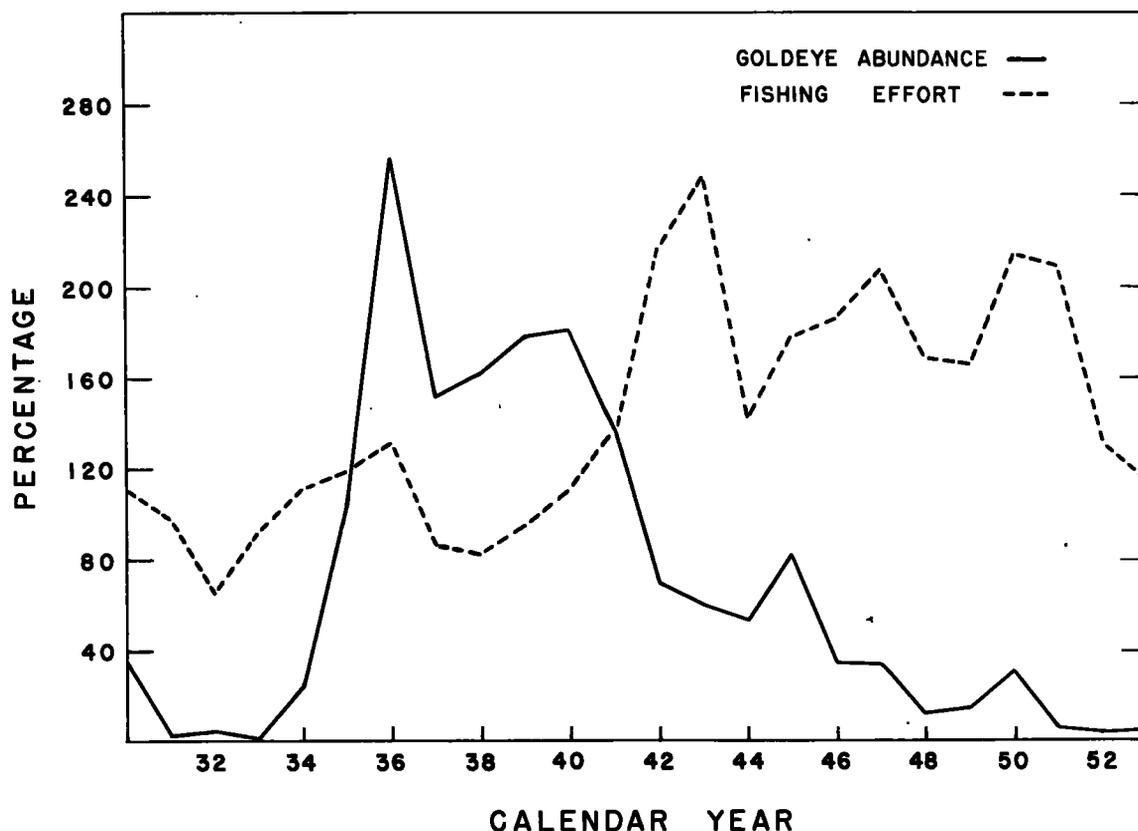


FIGURE 1.—The abundance of goldeye and the total fishing effort expressed as percentages of the 1931–40 average.

It therefore appears that the abundance of walleyes does not affect the abundance of goldeye directly. Similar appraisal of the possible influence of yellow perch on goldeye abundance failed to show a relationship. Since abundance indices of perch and walleyes fluctuate together and the estimates for the various years are based on fish of the same age groups in both species (Smith and Krefting, 1954), their combined influence on goldeye appears to be unimportant. Fluctuations in abundance of northern pike and other minor species did not appear to be related to changes in abundance of the goldeye.

Fishing Effort

During the 1930's when total fishing effort was at a low level, the wide fluctuations in goldeye abundance gave no evidence of correlation with changes in fishing effort. After 1940, however, the abundance declined steadily coincident with a substantial increase in fishing effort (table 2, fig. 1). Correlation of fishing effort with goldeye abundance 2 years later resulted in a significant nega-

tive coefficient ($r = -0.77, p < .001$).³ According to Van Oosten and Deason,⁴ the principal age groups in the 1937 commercial goldeye catches were the IV, V, and VI groups. In recent years, the predominant age groups have been III, IV, and V. This decrease in average age of the catch may be associated with an increase in fishing effort, but also may simply reflect the limited sampling and the characteristics of year-class strength at the time of the earlier study.

Where goldeyes have been subjected to commercial exploitation in Canadian waters, the populations have declined (Sprules 1947). Lake-of-the-Woods once supported a large goldeye population, which in recent years has nearly disappeared (Carlander 1949). The decline was accompanied by increased fishing effort although the goldeye was not particularly sought by commercial fishermen.

³ Since annual commercial catches of goldeye have been composed chiefly of a few age groups, it would be expected that any change in abundance due to change in fishing effort would appear in about 2 years.

⁴ Van Oosten, John, and Hilary Deason (MS.). A preliminary survey of the commercial fisheries resources of the Red Lakes, Beltrami and Clearwater Counties, Minnesota. The materials of this manuscript, much abbreviated, were the basis of a paper by Van Oosten and Deason (1957).

Although increased effort seems to be associated definitely with decline of the goldeye in the Red Lakes, as it has been in other waters, the mechanism of its influence is not clearly defined.

AGE AND GROWTH

Body-Scale Relation

Three to five scales, removed randomly from the region where the tip of the pectoral fin when rotated intersects the lateral line, were taken from 285 fish that ranged in length from 2.8 to 20.1 inches. The measurements of the projected images (28 ×) of all scales from each fish were averaged to obtain the estimate of scale length. Simple functions did not adequately represent the empirical data for the smaller fish, possibly because the number of measurements for fish 4.5 to 10 inches long was small; therefore, a line which appeared to fit all the data best was drawn by eye. Back-calculations of length were made from a nomograph constructed to incorporate the body-scale relation defined by this line (fig. 2).

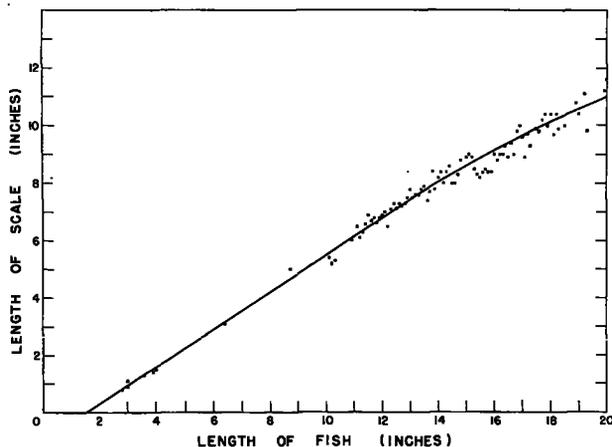


FIGURE 2.—The body-length/scale-length relation of Red Lakes goldeye, as plotted by eye from empirical points. (Scale measurements magnified 28 times.)

Calculated Growth

The growth rate of the Red Lakes goldeye is most rapid during the first 3 years of life, is reduced markedly in the fourth year, and declines steadily thereafter (fig. 3). Samples from the 1953 catch indicate that the rate of growth in both sexes decreased markedly in the fourth year, and that at the end of the fourth year and thereafter, the females exceeded the males in length (table 3).

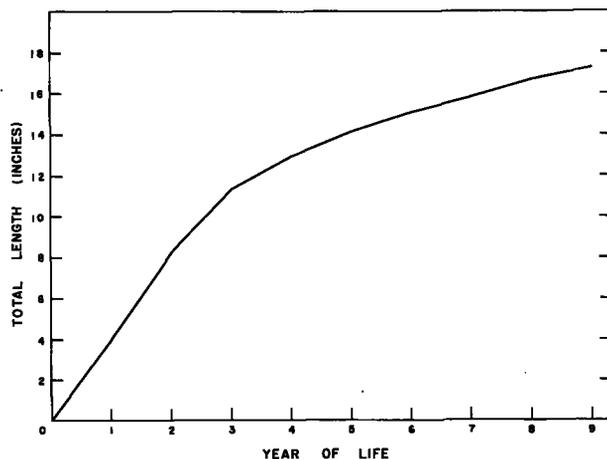


FIGURE 3.—Grand-average calculated length at the end of each year of life of goldeye from Red Lakes, sexes combined.

Slower growth of male goldeyes in the third and later years of life has been shown for Lake Texoma goldeyes (Martin 1952).

Comparison of the average calculated total lengths at the end of the first 3 years of life in the various year classes reveals only small differences, except in the 1941 and 1949 broods (table 4). Differences are greater after the fourth year of life, especially in the year-classes 1946 to 1949, which are considerably shorter at corresponding ages than are the later year classes. This difference apparently is caused by the cumulative effect of very poor growth in 1950 and 1951. The grand-average calculated total lengths of the fish captured in 1953 are shorter than the combined calculated lengths of the catches for all years except in the first year of life, because the 1953 catch was composed primarily of the year-classes 1946 to 1949. Goldeyes taken in 1937 and 1938 (Eddy and Carlander, 1942; Van Oosten and Deason; see footnote 4, p. 35) grew more slowly than those collected in the present study (table 5).

The marked differences in growth rate among year classes during the period of their greatest availability to the commercial gear would be expected to make considerable difference in the total contribution of the various year classes to the annual production. These changes would be especially apparent during periods of high population levels, but in recent years the harvest and abundance have been at such low levels that these changes were not important to the fishery.

TABLE 3.—Average total length of 288 goldeyes of the 1953 collection at time of capture and at time of annulus formation, by sex
[Length in inches]

Age and sex	Number of fish	Total length at capture	Calculated length at end of year of life—							
			1	2	3	4	5	6	7	
IV group:										
Male.....	32	12.5	4.82	7.63	10.56	12.25				
Female.....	53	13.3	4.63	7.36	10.20	12.36				
V group:										
Male.....	93	13.8	4.26	8.40	11.42	12.63	13.40			
Female.....	42	14.7	4.17	8.19	11.60	13.03	14.10			
VI group:										
Male.....	46	13.9	4.16	8.20	11.21	12.34	13.12	13.80		
Female.....	20	15.0	4.17	8.20	11.32	12.62	13.70	14.59		
VII group: Male.....	2	14.6	4.17	8.40	11.03	12.26	13.12	13.90	14.30	
Grand-average calculated length:										
Male.....			4.41	8.08	11.06	12.41	13.26	13.60	14.30	
Female.....			4.32	7.92	11.04	12.67	13.90	14.59		
Increment of average:										
Male.....			4.41	3.67	2.98	1.35	0.85	0.34	0.70	
Female.....			4.32	3.60	3.12	1.63	1.23	0.69		

TABLE 4.—Average calculated total lengths of 1,165 Red Lakes goldeyes sampled from the commercial catches, 1949-53
[Sexes combined; length in inches]

Year class	Date collected	Age group	Number of fish	Average calculated length at end of year of life—								
				1	2	3	4	5	6	7	8	9
1941.....	1949	VIII	9	3.7	8.2	10.8	12.4	13.5	14.4	15.4	16.0	
1942.....	1949-51	VII-IX	22	4.0	8.3	11.4	12.8	14.2	15.1	15.8	16.5	17.1
1943.....	1949-52	VI-IX	48	3.9	8.4	11.4	13.1	14.3	15.3	16.1	16.9	17.4
1944.....	1949-52	V-VIII	24	3.9	8.5	11.6	13.3	14.5	15.4	16.1	16.6	
1945.....	1949-53	IV-VIII	62	4.0	8.2	11.3	13.2	14.4	15.4	16.1	17.0	
1946.....	1949-53	III-VII	258	4.1	8.0	11.1	12.8	13.5	14.2	14.3		
1947.....	1949-53	II-VI	430	4.2	8.4	11.4	12.7	13.4	14.0			
1948.....	1951-53	III-V	190	4.2	8.5	11.7	12.8	13.7				
1949.....	1952-53	III-IV	122	4.9	7.6	10.6	12.3					
Grand average.....				4.1	8.3	11.3	12.9	14.1	15.0	15.8	16.6	17.2

TABLE 5.—Grand-average calculated total lengths, sexes combined, of goldeyes collected from the Red Lakes fishery in 1937-38 and 1949-53, and from Lake Texoma in 1949
[Length in inches]

Source	Date collected	Number of fish	Average calculated total length ¹ at end of year of life—							
			1	2	3	4	5	6	7	8
Eddy and Orlander (1942).....	1937	625	2.8	6.4	9.4	11.0	12.5	13.6		
Van Oosten and Deason (MS.) ²	1938	10	3.1	7.9	11.0	12.4	13.5	14.4		
Martin (1952).....	1949	817	7.5	8.8	11.2	12.6	13.2	14.2		
Present study.....	1949-53	1,165	4.1	8.3	11.3	12.9	14.1	15.0	15.8	16.6

¹ Standard lengths of the various authors were converted to total lengths through use of length conversion factor based on 361 Red Lakes goldeyes from present study. The ratio of standard length to total length was 0.815; the ratio of fork length to total length was 0.907.
² See footnote 4, page 35.

Comparison with Growth in Other Areas

Rawson (1947) reported that most goldeyes taken in Lake Athabaska were 6 to 11 years old and 12 to 16.5 inches long. Although the type of length measurement is not specified, it appears that these fish grow more slowly than those in Red Lakes. Bajkov (1930) presented growth data for goldeyes from several lakes in Manitoba. These data are not directly comparable with those from Red Lakes because information on the type

of measurement was omitted, but comparison of annual increments represented as percentage increase suggests slower growth, especially in the earlier years of life.

Lake Texoma goldeyes (Martin 1952) apparently grew much more rapidly in their first year than did fish from the Red Lakes; in later years of life, however, the average annual increments of growth and total lengths, with one exception, were greater in Red Lakes fish (table 5). The

TABLE 6.—Annual fluctuations in growth of Red Lakes goldeyes determined from sample years 1949 to 1953

[Expressed as percentage deviation from the mean annual increment of the entire sample from each year's collection in different calendar years]

Year collected	Percentage deviation in calendar year—										
	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
1949.....	-0.4	-7.0	6.7	1.6	-7.2	-0.9	1.4				
1950.....		0.3	2.5	6.2	-6.4	-5.0	3.5	-0.9			
1951.....					16.5	0.2	3.0	7.3	-26.8		
1952.....					20.4	2.9	5.6	8.0	-17.1	-19.8	
1953.....							9.2	7.2	-10.0	-16.1	9.5

apparent unusually large first year's growth of Lake Texoma goldeyes may result from use of the 4.5-inch intercept of the body-scale regression line.

Validity of Age Determination

False annular marks on the scales of all age groups and obscure patterns in the outer zones of those from older fish hampered accurate assessment of age. The best criterion of annuli was the cutting-over of circuli in the lateral and postero-lateral fields. Validity of age determinations for Red Lakes goldeyes was supported in three ways. First, the number of annuli increased systematically with increase in fish length in collections of separate years. Second, agreement was good among calculated lengths at the same age in various year classes (table 4) and was still better among calculated lengths of the different age groups of the same year classes. Third, different year classes collected in the same or different calendar years agreed with respect to the relative goodness or poorness of growth in certain calendar years. Percentage deviations of growth of Red Lakes goldeyes from the average annual increment of the period were determined separately for the samples of each year of collection, 1949 to 1953 (table 6). Although the base period is different for each year of collection, similarity among the trends gives considerable support to the validity of age determinations.

Relation Between Growth and Temperature

Water temperature may influence growth of fish directly by its effects on metabolism and behavior, indirectly through food production, or by a combination of these effects. Since temperatures in Red Lakes vary considerably in different seasons, changes in growth of goldeye could be related to this factor.

The relation between annual fluctuations in growth rate of Red Lakes goldeyes and mean air temperatures during the growing season, there-

fore, was evaluated by comparing the percentage annual deviations of each from the mean value for the period 1947-53 (table 7). This particular period was used because it did not include samples of less than 20 fish. Because the temperature of the shallow waters of the lake have been observed to be correlated very closely with air temperature, the mean air temperatures for June, July, and August (the major part of the growing season) were used. During the limited span of years available there was a positive correlation between fluctuations of summer temperature and rate of growth ($r=0.90$, $p=0.02$).

TABLE 7.—Percentage deviations of mean air temperature (June, July, and August) and of mean annual growth of Red Lakes goldeyes from the average for 1947-52

Item	Percentage deviations in calendar year—					
	1947	1948	1949	1950	1951	1952
Growth of goldeyes.....	6.1	12.9	10.8	-11.7	-15.4	-2.8
Mean air temperature..	3.1	1.0	3.1	-3.8	-3.9	0.4

Age and Size at Maturity

Few data are available on the size and age at which goldeyes reach maturity. Dymond⁵ stated that in some Manitoba lakes females spawn first when 4 years old, at a length of 12 inches and a weight of 12 ounces, but many do not mature until a year later. A few males mature at 3 years. Among the 10 goldeyes from the Red Lakes which were examined by Van Oosten and Deason (see footnote 4, p. 35) in 1938, 3 were mature males belonging to age-groups III, IV, and VI. The remaining 7 fish were females of which 4 were immature (age-groups II, III, and V) and 3 were mature (age-groups IV, V, and VI). In the present study, 34 male and female goldeyes, all of age-groups IV and V, examined in late July and early August were mature. From

⁵ Dymond, J. R. The goldeye, its life history and conservation. 8 pp. (typewritten).

observations on Lakes Winnipeg and Winnipegosis, Hinks (1943) reported that only about half of the female goldeyes, 12 inches or longer, spawned in any one year.

Length-Weight Relation

A description of the length-weight relation in goldeyes of the Red Lakes was based on 156 specimens. No significant differences between the sexes were noted. The relation is expressed by the formula—

$$\log W = -2.094 + 2.844 \log L,$$

where

W = weight in ounces,

and

L = total length in inches.

STRUCTURE OF THE EXPLOITED GOLDEYE POPULATION

Since nearly all samples used in the present study were taken from commercial catches, they represented the portion of the goldeye population

that was available to the commercial gear. In 1953, the origin of samples (whether from Upper Red Lake or Lower Red Lake) was recorded. Because age and length-frequency distribution of samples from both lakes were similar, it was assumed that samples from mixed catches were suitable for the analysis of population structure. Length distributions and age frequencies were similar from month to month in all years.

Length Distribution of the Commercial Catch

The length-frequency distribution of the commercial goldeye catch was based on 2,787 randomly selected fish taken in 1949-53 (fig. 4). With one exception, the distribution showed an increase in the average length of the predominant size groups in successive years (table 8). This increase in average length reflects dominance of a few year classes in the catches.

The 3½-inch-mesh commercial gill nets took fish over a wide range of lengths (10.0 to 19.4 inches), but the major part of the total catch was composed of fish in the lower half of the range

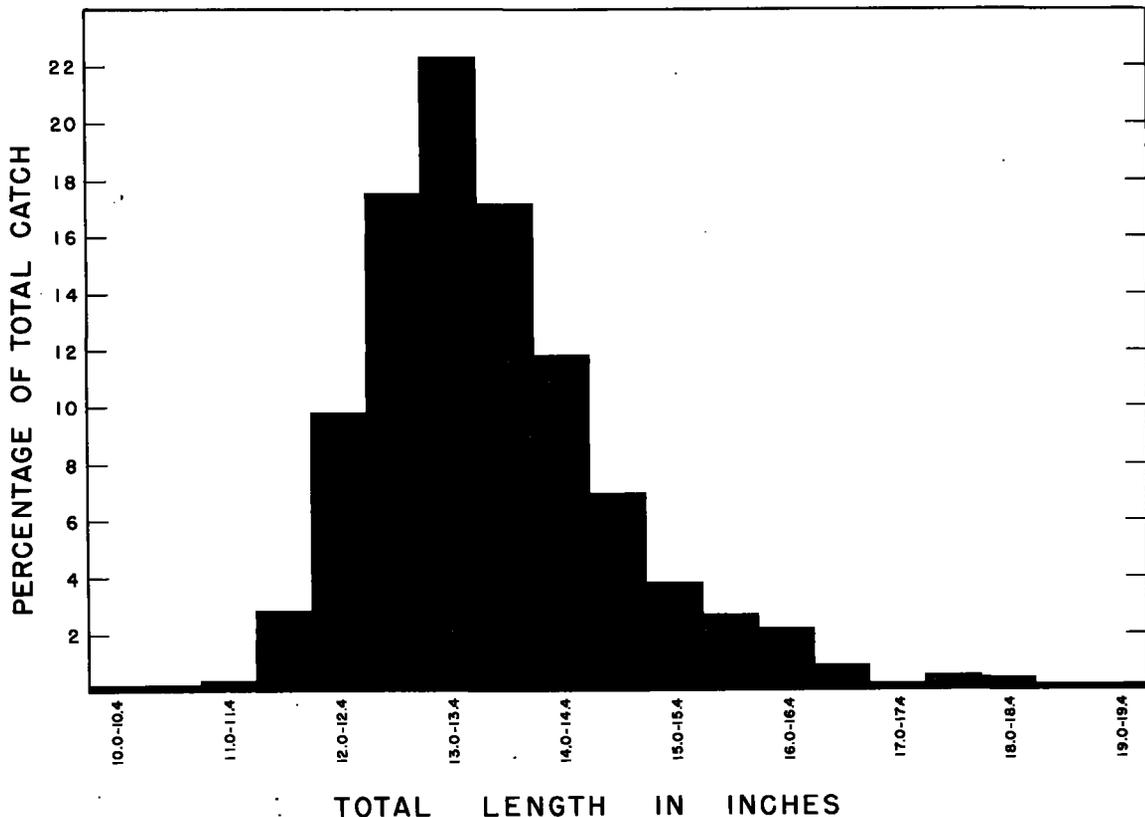


FIGURE 4.—Length-frequency distribution of the commercial catch of Red Lakes goldeyes, all samples combined.

TABLE 8.—Length-frequency distributions of goldeyes taken from Red Lakes commercial catches, 1949-53

[Modes indicated by asterisk*]

Total length (inches)	Frequency of occurrence of fish collected in—					Total
	1949	1950	1951	1952	1953	
10.0-10.4	2	1				3
10.5-10.9	1					1
11.0-11.4	3	3	1		1	8
11.5-11.9	39	15	9	9	7	79
12.0-12.4	*75	33	119	20	27	274
12.5-12.9	40	38	304	47	63	492
13.0-13.4	14	*46	*316	*155	91	*622
13.5-13.9	9	33	160	144	*134	450
14.0-14.4	5	7	74	102	128	330
14.5-14.9	4	7	40	47	98	196
15.0-15.4	6	7	29	17	48	107
15.5-15.9	*23	11	22	6	13	75
16.0-16.4	12	*23	14	6	5	60
16.5-16.9	4	9	5	2	2	22
17.0-17.4	1	2	2	1	1	7
17.5-17.9	2	3	6	4		15
18.0-18.4		2	3	3	2	10
18.5-18.9		1	3			4
19.0-19.4	1		1			2
Total	241	255	1,108	563	620	2,787

(fig. 4). The Red Lakes goldeyes first become completely available to the commercial gill nets within the size interval 13.0 to 13.4 inches total length. Although it has not been definitely determined, there is some indication that the larger fish may not be completely available to the gear.

Age Composition of the Commercial Catch

The age composition of the commercial goldeye catches was described from 1,578 fish. Age frequencies, determined from scales, were tabulated in 0.5-inch intervals to permit extension of the data to samples for which only length measurements were available. Approximately 83 percent of the commercial catch during the period 1949-53 consisted of III-, IV-, and V-group fish; age-group IV contributed 38.4 percent and age-groups III and V comprised approximately 20.7 percent and 23.8 percent of the total (table 9). The remainder

TABLE 9.—Age distribution of 1,578 goldeyes from commercial catches in the Red Lakes, 1949-53

Year collected	Percentage ¹ in age-group—									
	II	III	IV	V	VI	VII	VIII	IX	X	XI
1949	0.8	66.4	10.0	3.3	5.8	5.8	3.7		0.5	
1950		25.7	47.8	3.5	5.1	11.4	2.3		0.9	
1951		0.9	77.1	15.1	3.7	0.5	0.3	0.2		
1952		9.6	28.6	52.4	6.7	1.4	0.3	0.5		0.1
1953			28.5	43.9	26.0	0.5	0.7			
Combined samples	0.2	20.7	38.4	23.8	9.5	3.9	1.4	0.1	0.3	

¹ Differences between summation and 100 percent represent fish which could not be aged.

of the catch was made up principally of VI-, VII-, and VIII-group fish.

The commercial catch in 1937 (Van Oosten and Deason; see footnote 4, p. 35) was dominated by age-groups IV, V, and VI, which comprised approximately 25 percent, 39 percent, and 20 percent of the total catch. Age-group III made up about 9 percent and the VII and VIII age groups contributed 5.9 percent and 0.5 percent of the total.

Strength of Year Classes

The catches from 1949 to 1952 were largely dependent on one or two age groups of the 1946, 1947, and 1948 year classes. The take in 1953 was derived chiefly from the combined catch of the 1947, 1948, and 1949 year classes. In contrast, during 1949 when abundance was three times as large as that of 1953, the catch was largely based on the 1946 year class (tables 2 and 9). The presence of unusually strong or weak year classes can affect markedly the catch in any season, since the annual harvest is dependent on the abundance of very few age groups. Although the size of year classes in recent years has been small in comparison with the hatches responsible for the greater abundance in earlier years, the number of age groups comprising the annual harvest apparently has changed little.

Sex Ratio

Males consistently outnumbered females in daily samples from the goldeye catch of 1953: in a total of 389 goldeyes, 56 percent (220) were males and 44 percent (169) females. The ratio of males was even higher (70 percent) in the age-groups V and VI which were completely available to the gear. Females outnumbered males in age-group IV as might be expected, since IV-group males in 1953 were below the size of complete availability (table 3)

FOOD HABITS

Food of the goldeye, as reported by a number of previous investigators, consists chiefly of a wide variety of insects. Examination of 34 stomachs in the present study indicated that the principal food organisms were aquatic insects (larval and adult). The common occurrence of terrestrial insects suggests that goldeyes are frequently surface feeders in shallow water. Bajkov (1930) concluded that goldeyes foraged chiefly at night since large quantities of deep-

water organisms, which rise to the surface at night, were found in their stomachs. In marshes around the Saskatchewan River, movements of young fish were found to be greatest near sundown and sunrise and activity was generally greater at night than during the day (Sprules 1947). In the present study, the common occurrence of noctuid moths and fireflies in stomachs suggests that goldeyes in the Red Lakes are often nocturnal feeders.

CONCLUSIONS

The appraisal of fluctuations in abundance of the various fish populations in Red Lakes yields no evidence that the recent decline of goldeyes is attributable to an increase in the number of walleyes and yellow perch, which are the predominant species. The lower abundance of goldeyes in recent years has been accompanied by increased fishing effort, as has been observed elsewhere, but the actual influence of this factor is not clearly defined. The abundance of the goldeye population is now extremely low, but it may recover as it did in the 1930's. The recent capture of first-year fish in shore seining lends some support to this view. Available information suggests that the only change in management practice which might aid in the recovery of the population would be a reduction in fishing effort. Under present conditions, gill nets are fished primarily for the walleyes and secondarily for the perch; catch of other species is incidental. Special management of the goldeye, therefore, would not be practical unless entrapment gear of some type were employed.

Demonstration of the validity of age determination and appraisal of growth difference in various year classes have shown that prediction of available commercial stock would be possible if adequate sampling of the population prior to its entrance into the fishery could be obtained. As has been shown for various other species, the strength of individual year classes in large measure determines

the size of the stock available for harvest in any particular year.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
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FOOD OF THE SQUAWFISH
Ptychocheilus oregonensis (Richardson) OF THE
LOWER COLUMBIA RIVER

BY RICHARD B. THOMPSON



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ABSTRACT

A study is presented of 3,546 stomachs of the squawfish, *Ptychocheilus oregonensis* (Richardson), collected from April 1955 to April 1956 in the lower Columbia River. The basic food table of the squawfish, based on a modified point system with emphasis on salmon predation is presented. Sixty-three percent of the stomachs examined were empty. Size of squawfish, season of the year, and geographical distribution within the river affect the occurrence and importance of the food items.

Major food items were fishes, crayfish, and insects, and, in much lesser amounts, plant materials, mollusks, and miscellaneous items. Squawfish from 3 to 8 inches long subsisted on a diet of insects; above that length fishes and crayfishes attained importance. At 11 inches, fishes and crayfishes were dominant and insects were only 5 percent of the stomach content.

All occurrences of juvenile salmon in squawfish stomachs were related to releases of young salmon from hatcheries. The role of the squawfish as a predator on salmon was limited to time and place where juvenile salmon concentrations were high following release.

FOOD OF THE SQUAWFISH, *Ptychocheilus oregonensis* (Richardson) of the Columbia River

By RICHARD B. THOMPSON, *Fishery Research Biologist*, BUREAU OF COMMERCIAL FISHERIES

An average of 56 million young salmon has been released annually into the Lower Columbia River¹ during the past 5 years from Federal and State fish-cultural stations and hatcheries. These young salmon varied from unfed fry of about 1½ inches long to fingerlings of 5½ inches. At the time of their release into the river, the young and relatively defenseless salmon are in dense concentration and therefore easy prey for predatory fishes. Before the dispersal of the salmon into the turbid water of the main Columbia River, they are particularly vulnerable to predators.

Numerous observations of predatory fish actions on the small salmon immediately after their release have been made by hatchery personnel. Some control measures on the predator populations have been attempted with gill nets and dynamite. The most abundant predator collected was the Columbia River squawfish, *Ptychocheilus oregonensis* (Richardson).²

As a result of the indications of predation cited, a program of study was initiated by the Columbia River Fishery Development Program which had as one of its activities an investigation of the role of the squawfish as a predator on young salmon in the Lower Columbia River.

The first phase of the study was to examine the distribution of the species in the Lower Columbia River and its tributaries, particularly with respect to the location of present and planned salmon hatcheries and fish-cultural stations. Included in this phase was the examination and analysis of the basic foods of the squawfish. The present food study is based on the examination of the

stomachs of squawfish taken in the distributional-study collections. The fish were collected from the mouth of the Columbia River at Astoria (Oreg.) to McNary Dam, 180 miles east of Portland (Oreg.) and some 240 river-miles from the mouth. These sampling operations were conducted from April 1955 to April 1956, inclusive.

The second phase of the planned operation was to conduct a more detailed study of the life history of the squawfish in a smaller area. This was done by employees of the Columbia River Fishery Development Program and will be reported on at a later date.

The purpose of the present food analysis is to determine the basic foods of the species within the study area. In addition, if losses of salmon to squawfish were found to occur in appreciable numbers, it was desired to determine where and at what times these losses were the highest. The collection of squawfish stomachs was not designed for a detailed study of diet, but to determine the basic foods of the species. A time-consuming attempt at detailed accuracy in the stomach analysis was not advisable, hence the more rapid, but admittedly less accurate point system of stomach-content evaluation was selected for use.

REVIEW OF LITERATURE

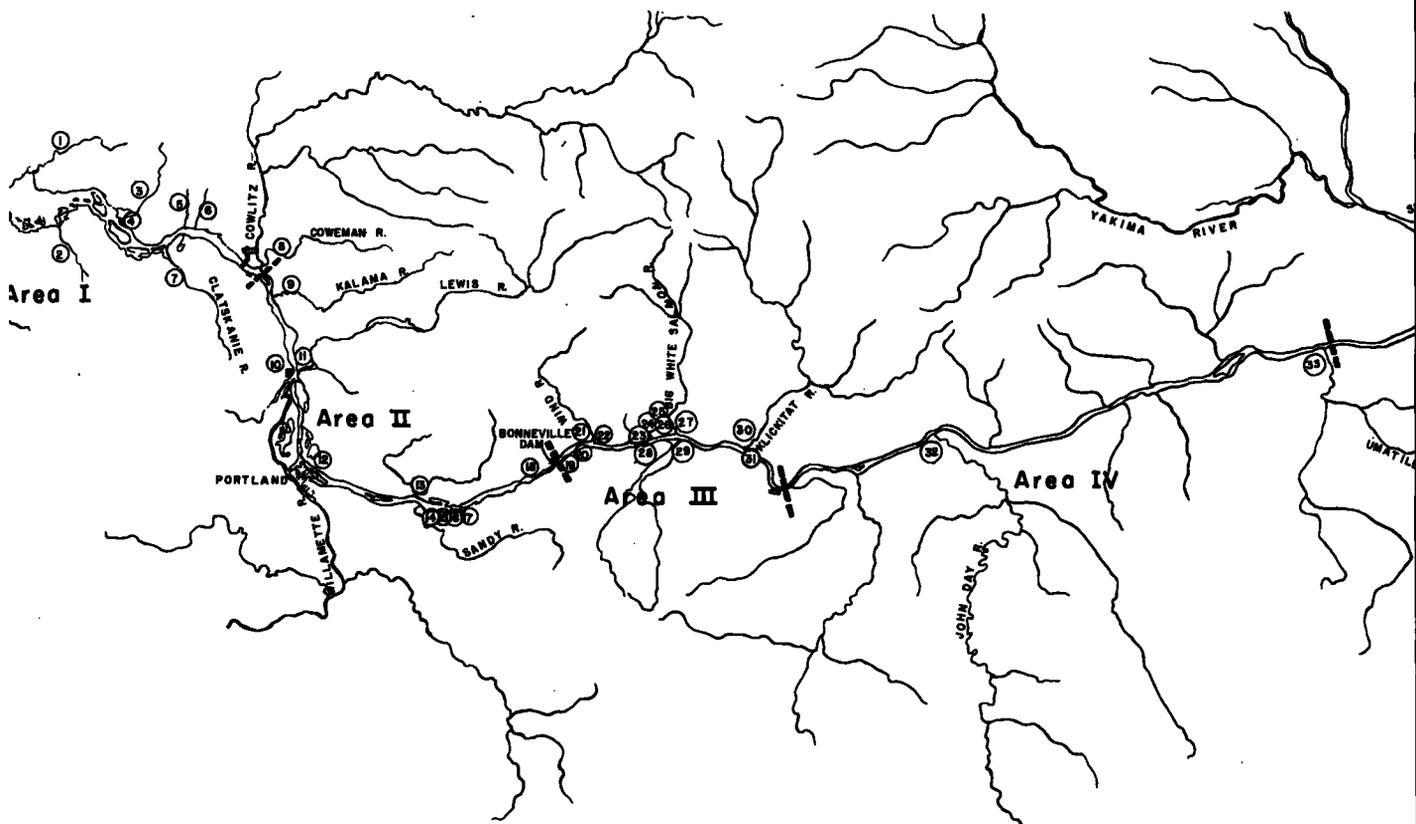
Little information is available on the life history and food habits of the squawfish in the Columbia River. Very few food studies have been made on the species. Most of the recorded information has been obtained from collections made in British Columbia, Canada.

Clemens and Munro (1934), in a food study of the squawfish from central British Columbia, examined stomachs from 119 squawfish that ranged in size from 1½ inches to 12 inches. They determined that the smaller squawfish up to 4 inches in length fed entirely on aquatic insects and other

¹ Progress Report, Fiscal Year 1956. Fishery Development Program of the Columbia River. U.S. Fish and Wildlife Service, Portland, Oreg. 66 pp.

² Observations on hatchery releases and squawfish predation in Little White Salmon River in the spring of 1953, by Paul D. Zimmer. Issued by U.S. Fish and Wildlife Service Regional Office, Portland, Oreg. August 1953 (mimeographed).

NOTE.—Approved for publication Apr. 23, 1958. Fishery Bulletin 158.



Sampling stations where no squawfish captured indicated by blocks; area boundary defined with dashes.

- | | |
|--------------------|----------------------------|
| 1 Grays River | 18 Beacon Rock |
| 2 Big Creek | 19 Eagle Creek |
| 3 Elokomin Creek | 20 Herman Creek |
| 4 Cathlamet | 21 Upper Wind River |
| 5 Abernathy Creek | 22 Wind River (mouth) |
| 6 Germany Creek | 23 Dog Creek |
| 7 Clatskanie River | 24 Drano Lake |
| 8 Coweman River | 25 "Drinking Fountain" |
| 9 Kalama River | 26 Spring Creek |
| 10 St. Helens | 27 Big White Salmon River |
| 11 Lewis River | 28 Broughton Drift Area |
| 12 Portland | 29 Hood River—Wells Island |
| 13 Washougal River | 30 Klickitat River |
| 14 Sandy River | 31 Lyle Drift Area |
| 15 Corbett | 32 John Day River |
| 16 Vista Slough | 33 Umatilla River |
| 17 Oneonta Creek | |

FIGURE 1.—Columbia River and tributaries showing location of gill-net sampling stations and subarea boundaries.

invertebrates. A few individuals as small as $4\frac{1}{2}$ inches fed on fishes, but squawfish of all sizes contained insects at certain times of the year. Of the 119 squawfish, 67 had eaten fish and 27 of these had eaten young salmonoids (salmon, trout, and kokanee).

Chapman and Quistorff (1938) examined 95 squawfish stomachs collected in the north-central Columbia River in the State of Washington. All but 37 of these were empty; 9 contained fish remains, none of which were identifiable as salmonoids. The remainder of the food items were prin-

cipally aquatic insect life. The diet of the squawfish was not unlike that of the rainbow trout taken in the same area.

Ricker (1941), as a result of long-term studies on Cultus Lake, tributary to the Fraser River in British Columbia, determined that the squawfish, because of its abundance and predatory habits in that lake, exacted the greatest toll of all predators on the sockeye salmon (*Oncorhynchus nerka*) fry and fingerlings residing in the lake prior to their departure for the sea. During the winter the young salmon formed the main food of squawfish larger than 4½ inches. During the summer the squawfish fed on other fishes (small cyprinids and sculpins) presumably because of the absence of young salmon in the waters frequented by the squawfish. The number of salmon consumed per squawfish was low, commonly 0.2 to 0.4 per stomach, but the abundance of squawfish made them the foremost predator in the lake. A systematic removal program was initiated principally against the squawfish and charr (*Salvelinus malma*) and by 1938 it succeeded in reducing the number of squawfish to one-tenth of their 1935 level. As a result of the removal of predators, the authors reported sockeye survival to the migrant stage increased threefold (Foerster and Ricker, 1941).

The squawfish have been considered a significant agent affecting the abundance of sockeye salmon of Lakelse lake, British Columbia (Brett and McConnel, 1950). Six hundred and twenty-three squawfish were collected with gill nets and the stomachs examined. Sockeye salmon contributed 31 percent, by volume, to the squawfish stomach contents during the summer months. The calculated losses of salmon within the lake, from fry to migrant size, were accounted for by an estimated consumption of 140 salmon per predator per year, a figure which was accepted as reasonable.

Studies on the closely related Sacramento River squawfish (*Ptychocheilus grandis*) by Taft and Murphy (1950) suggested that the squawfish prey on young trout and compete with trout of all sizes for food.

MATERIALS AND METHODS

Squawfish stomachs examined in this study were obtained by field crews of the Columbia River Fishery Development Program during the period April 1955 to April 1956. The fish were taken

preponderantly by gill nets set at 36 sampling stations established along the Columbia River from Astoria, at the mouth, to the vicinity of McNary Dam, and in the lower reaches of selected tributary streams.

Observations recorded by the U.S. Corps of Engineers at Bonneville Dam indicate that during the period of squawfish sampling river conditions, compared with the conditions of other years, were normal. (Corps of Engineers, 1955.)

Mesh sizes of the gill nets ranged from 1½ inches to 4 inches, stretched measure. The nets differed slightly in type and usage; most were set nets, which were anchored in place with the lead line on the bottom of the river. Fishing in certain areas was conducted with nets that drifted with the current; minor squawfish catches were made with these drift-type nets.

The set nets were set during the day, left to fish overnight, and examined the following day. Sampling in this manner was conducted throughout the study period, with minor exceptions for the repair of nets and gear. The sampling crews moved from one set of adjacent stations to the next upstream sites; continuing until the upper sampling stations were completed, then starting again at the downstream stations. A complete survey of all stations was completed approximately each month.

The stomachs of 3,546 squawfish were collected and examined in this study.

Figure 2 shows the length-frequency distribution of the 3,546 squawfish examined in the food study. The immature and unknown category includes the small fish that could not be sexed by visual inspection and also mature fish, the sex of which was unreported. The consideration of the percentage occurrence and percentage composition of foods by each length class reduces the bias of the results caused by variations in sample length composition. The sampling covered a wide enough range of seasons, water conditions, habitats, and fish sizes to provide reliable data on the basic food and feeding activity of the squawfish in the Lower Columbia River during the time of sampling.

A solution of 70 percent alcohol was injected into the stomach of each fish as soon as it was removed from the net. The amount of alcohol inserted depended on the size of the fish, but was

Immature and unknown, 1,043; males, 1,307; females, 1,196; total, 3,546.

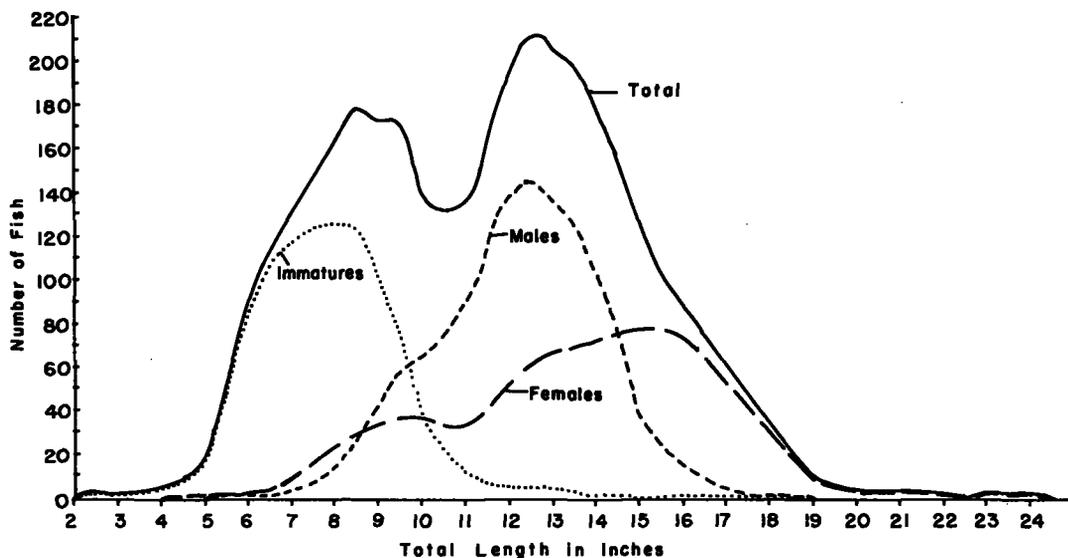


FIGURE 2.—Length-frequency distribution of squawfish in food analysis, by sexes and total. Grouped to $\frac{1}{2}$ -inch-length classes and smoothed by a moving average of three.

seldom more than 10 milliliters. The preservative was necessary to stop digestive action on the stomach contents, for digestion was found to proceed at a rapid rate after the fish had been removed from the water, especially in warm weather. A few untreated stomachs collected early in the study were discarded because the contents had been digested.

The fish were measured on a measuring board to the nearest one-tenth of an inch and weighed to the nearest one-hundredth of a pound. Following this, they were sexed and the degree of maturity noted and recorded. The stomachs were then removed and preserved for later examination.

The procedure followed in examining the stomachs was as follows: first, the stomach food volume was estimated and points allotted; second, the contents of the stomach were placed in a petri dish for identification and evaluation of the individual food items. Each food item was identified as specifically as possible, although no extensive taxonomic classification was attempted on insects, plant materials, and miscellaneous items.

EVALUATING FOOD ITEMS

The three generally accepted methods of assessing the stomach contents of fishes are by number,

by occurrence, and by some measure of the comparative or actual volumes of the food items. The use of only one of these three methods provides only partial information of feeding habits. Some combination of the three must be used to determine accurately the food and feeding habits of the species.

The numerical system is the most simple. It is a direct count of the various food items found in the stomachs. This, however, tends to place undue emphasis on small items and perhaps those foods that are most resistant to digestion. The small items with numerical dominance may make up only a small portion of the bulk of the foods. The time involved in making the counts and the errors involved in attempting enumeration of broken and partially digested items made the use of such a system inadvisable for the purposes of this study.

The frequency of occurrence of a food item is the number or percentage of fish in the sample which contained a given food item. The statistic may be a measure of the feeding selectivity and food availability to the feeding fishes. These two factors are considered together in this report.

The volumetric system is based on the bulk of food items found in the stomachs. Conditions affecting the size of items after ingestion, such

as the rate of digestion and elapsed time, may distort the results, placing emphasis on the recently eaten and more durable items. However, a large series of samples over a period of time should show with reasonable accuracy the average volume of food items eaten. The volumetric determination of the diet of a species of fish does not indicate the nourishment received from the various food items. Until dietetic values of the items are determined for each consuming species, volume seems to offer the best criterion.

Numerous variations of the basic volumetric analysis have been developed for food investigations with different specific purposes. The point method was first used by Swynnerton and Worthington (1940), who listed the individual food items in each fish stomach as "common," "frequent." They used rough counts and judgment of volume by eye to determine each item's importance in the stomach. Each food category was allotted a number of points based on its importance in the stomach and these points were summed and reduced to percentages. This gave the percentage composition of the various foods in all the fish examined. The technique was basically volumetric, the rough counts of organisms being adjusted as to their size to make one large organism count as much as a great number of small items.

Hynes (1950), in a study of the food of sticklebacks of the British Isles, developed a method of food assessment based on volumetric estimation. Hynes considered a full stomach to be valued at 20 points, but allotted values of only 1, 2, 4, 8, and 16 points. No intermediate values were used, since he felt that the technique was only approximate and no additional flexibility was necessary. The author recognized the difficulty that when a full stomach containing only one kind of food was found it received only 16 points, rather than the 20 points a full stomach should have received. However, few of the large number of sticklebacks examined in his study contained only one food item and he found that the results of the technique corresponded closely with results obtained by other methods of assessment. Hynes recommended that "... in future work it would be better to allot the points to the stomach in the first instance, and then to subdivide the number allotted to the various food items present."

Hynes lists the favorable factors of this type of evaluation: "... it is rapid and comparatively easy, it requires no special apparatus for measurement, it is not influenced by frequent occurrences of small organisms in small numbers, nor of heavy bodies, and does not involve trying to count large numbers of small and broken organisms." He further stated that it does not give the spurious impression of detailed accuracy which is given by some other methods.

The author cited as the technique's major shortcomings the subjectiveness of the investigator and the influence of prejudice in the allotment of points. However, he continued, "... where large numbers are analyzed over a period of months this difficulty is to some extent overcome." In examining a large series of stomachs, the investigator becomes experienced in estimating their fullness. However, the identification of the food items does not become any less important and the investigator must continue the careful identification of remains of organisms as specifically as possible. These criticisms apply equally well to other methods of food assessment.

The present assessment of the stomach contents of the squawfish of the Lower Columbia River is based on Hynes' technique, with slight modification.

Immediately after being opened, each squawfish stomach was evaluated according to its degree of fullness and allotted a certain number of "stomach points." A full stomach was valued at 20 points. No food values of less than one point were given; an empty stomach received zero points. No consideration of the comparative sizes of the stomachs was made, it being assumed that a full stomach was just as important to a small fish as was a full stomach to a large fish. However, since stomach size could have an effect on the extent of predation, the numbers of salmon and all other fishes found in the stomachs were counted. Thus the distorting influence of predator-size on predator-capability was to some extent overcome. These counts of the salmon remains supplemented the use of the points system in establishing the predatory role of the squawfish.

After the points were allotted to each stomach for its degree of fullness, the points were distributed among the individual food items present.

Each food category present was allocated points according to its relative volume in the whole of the stomach contents. In this manner, volume became the foremost consideration in evaluating the contents of the stomachs. The allotment of the stomach points prior to the evaluation and identification of the food items prevented the possibility that large, relatively undigested items, such as fish and crayfish, might lead the investigator to overestimate their volumetric importance. No attempt was made to evaluate partially digested remains on the basis of their volume when first eaten. Items were scored only by their volume when the stomach was examined.

During the early course of the investigation it became apparent that the point and percentage values were weighted too heavily for the rather small volume of food found in the stomachs. The technique of assessment did not take into proper consideration the lack of food in the entirely empty stomachs nor in those stomachs only partially filled with food.

In order to give the food items a point value corresponding accurately with their actual relation to the potential stomach volume, a modification of the basic point system was devised. An estimate of the maximum possible total of points attainable by the fish in a sample was calculated by multiplying the number of fish examined by 20, the food value of a stomach when full. An estimate of the "empty" volume was determined by subtracting the points gained by all the food items from this maximum possible total. The volume percentages were then determined for each food category, including "empty," from this maximum possible total and not the food point total. An example of the point system of food assessment for a four-fish sample is illustrated in table 1.

This estimation of the potential volume of a fish's stomach is a rough estimate of capacity. It is a necessary consideration, however, when the basic diet and the feeding activities of predatory fishes are under investigation and the results from the sample are applied to the general population. At the time of examination of the stomach, only the points gained by the food present were estimated. No direct estimate of "emptiness" was made for an individual stomach. When the stomachs for any given samples were grouped, the

TABLE 1.—*Example of the point system of food assessment for a 4-fish sample*

Fish No. and stomach volume	Food points allotted	Stomach contents	Food item points	Percentage composition
1. Full.....	20	2 sculpins.....	20	25.00
2. Two-thirds full...	13	1 lamprey larvae...	8	10.00
		10 Caddis larvae...	5	6.25
3. One-half full.....	10	1 rainbow trout...	6	7.50
		2 crayfish, small...	4	5.00
4. Empty.....	0			
Total.....	43			(53.75)
Maximum possible Empty.....	(4) × (20) = 80			
	80 - 43 = 37	Empty.....		46.25
				100.00

potential capacity was then calculated to arrive at an estimate of the "empty" volume in the sample.

Stomach volume can be increased greatly by stretching the stomach walls from a rather thick, folded state when the stomach is empty to a thin membrane when full. The maximum extension of the walls and the capacity of the stomach can only be estimated. The allotment of points to the volume of food items present was based on experience gained through the examination of hundreds of stomachs with a variety of volumes and foods.

The roughness of the capacity estimate detracts little from its value as used in this study. Here its basic use is to obtain an estimate of feeding activity by the populations of squawfish. Without it, application of the results of sample stomach analysis to the general population is impossible.

The problems of stomach contents analysis and methods of presentation are difficult ones and should be approached anew with each species and purpose of study. As Reintjes and King (1953) stated, "Regardless of the method of analysis used, there are many uncontrollable variables inherent in food studies which detract from the precision of the results. One may safely conclude, however, that those food items that rank large in number, large in volume, and high in frequency of occurrence are important foods . . . at the time and in the area sampled."

RESULTS

The detailed results of the study of the food of squawfish from the Lower Columbia River are shown in table 2. Numbers of items were obtained only for the fishes occurring in squawfish stomachs. No attempt was made to obtain counts

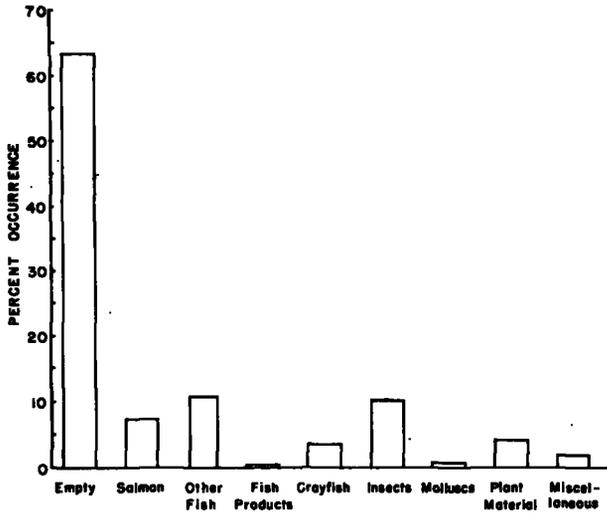


FIGURE 3.—Percentage occurrence of food items in 3,546 squawfish stomachs from the lower Columbia River.

of individual items of other foods. The main purpose of the study was to determine the basic food table of squawfish populations and an understanding of the role played by the squawfish as salmon predators. The counts of consumed fishes aid in determining this. Counts of small, nonfish items would have been time consuming, inaccurate, and would have offered only supplemental information to the main purpose of this study.

Of the 1,272 countable fishes found in the stomachs examined, 1,102, or 87 percent, were salmon. Sculpins comprised 6 percent, lamprey larvae 2.5 percent, and other species, mostly cyprinids, made up the remaining 4.5 percent.

Figure 3 shows that 63 percent of all the squawfish stomachs examined were totally empty. A measure of the emptiness of the stomachs only partially filled with food is not possible with this method of assessment.

The percentage composition is the evaluation of the importance of the food items as based on the modification of Hynes' (ibid.) "points" method. These point totals were grouped into the major food categories, and expressed as percentages of the total possible number of points, which included "empty" values. The inclusion of the points for emptiness illustrates not only what food was found and in what comparative volume but also the extent of overall feeding activity and food availability to the squawfish. Figure 4 illustrates the percentage composition of the foods

TABLE 2.—Results of the stomach analyses of 3,546 squawfish, *Ptychocheilus oregonensis*, from the Lower Columbia River

Food item	Number of items	Stomachs in which item occurred		Food "point" total	
		Number	Percent	Number	Percent
FISH					
Salmon and salmon remains.....	1,102	265	7.47	2,548	3.6
Sculpin, <i>Cottus</i> spp.....	80	65	1.83		
Lamprey.....	30	21	.59		
Trout, <i>Salmo</i> spp.....	16	11	.31		
Sucker, <i>Catostomus</i> spp.....	8	7	.20		
Chiselmouth, <i>Acrocheilus alutaceus</i>	20	9	.26		
3-spined stickleback, <i>Gasterosteus aculeatus</i>	8	5	.14		
Chub, <i>Mylocheilus caurinus</i>	3	3	.08		
Squawfish, <i>Ptychocheilus oregonensis</i>	1	1	.03		
Shiner, <i>Richardsonius balteatus</i>	4	4	.11		
Adult salmon carcass remains.....		23	.65		
Unidentifiable fish remains.....		234	6.60	12,870	14.0
Sum.....	1,272	648	18.27	5,418	7.6
FISH PRODUCTS					
Salmon viscera.....		1	.03		
Salmon ova (eyed).....		4	.11		
Salmon eggs (bait).....		5	.14		
Fish refuse.....		4	.11		
Sum.....		14	.39	193	.3
CRUSTACEA					
Crayfish.....		128	3.61	1,027	1.5
INSECTS					
Plecoptera.....		38	1.07		
Odonata.....		14	.39		
Trichoptera.....		46	1.30		
Diptera.....		7	.20		
Hymenoptera.....		11	.31		
Coleoptera.....		10	.28		
Unidentifiable insect remains.....		235	6.63		
Sum.....		361	10.18	1,567	2.2
MOLLUSKS					
Snails.....		13	.37		
Clams.....		19	.54		
Sum.....		32	.91	139	.2
PLANT MATERIALS					
Algae.....		79	2.23		
Wheat kernels.....		27	.76		
Unidentifiable plant remains.....		48	1.35		
Sum.....		154	4.34	701	1.0
MISCELLANEOUS					
Annelids.....		5	.14		
Stones and pebbles.....		3	.08		
Mud and detritus.....		43	1.21		
Feathers.....		1	.03		
Rodents (fur and remains).....		6	.17		
Salamanders.....		2	.06		
Sum.....		60	1.69	298	.4
Empty.....		2,243	63.25	61,587	86.8
Grand total.....				70,920	100.0

¹ Totals for all nonsalmon fishes.

of the squawfish stomachs examined. From it and from table 2 it is evident that the squawfish are omnivorous; probably they are opportunistic omnivores, willing to eat anything available that is palatable. However, fishes were the most important food item in both occurrence and composition.

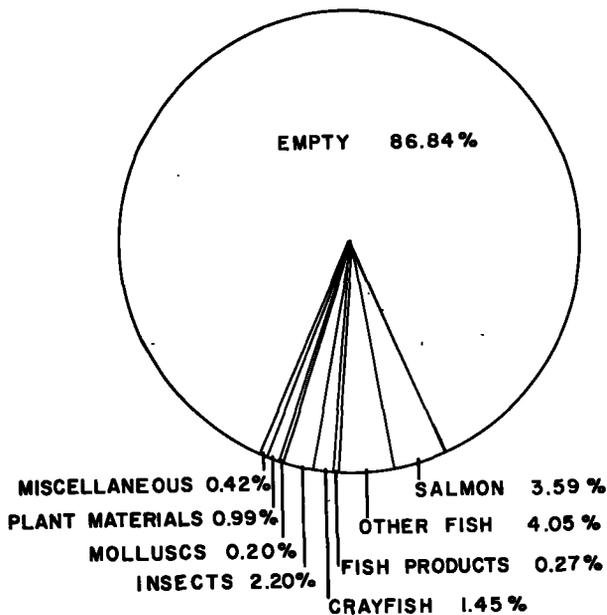


FIGURE 4.—Composition of contents from 3,546 squawfish from the Lower Columbia River.

Salmon were by far the most important genus of fish found in the entire sample. Insects, crayfish, and plant materials, in that order of importance, were the only other important categories of food. An interesting point from figure 4 and table 2 is that 87 percent of the estimated potential volume of the squawfish stomachs was empty.

Size of organisms eaten

The squawfish stomachs examined indicated that the fish are largely nonselective as to the sizes of organisms eaten. Smaller fish, of course, are limited to the smaller food organisms; however, larger squawfish showed evidence of feeding on small organisms also.

Algae, wheat kernels, and small insect larvae were found in the stomachs of some large fish, objects of small size in relation to the size of the fish and to other items of food.

The smallest items found in the stomachs were bits of green algae. These were usually found in conjunction with other items of food and may have been taken incidentally, but some stomachs contained only algae. The largest food items were fish. One squawfish, 18 inches in total length, had an 8-inch Columbia River chub, *Mylocheilus caurinus*, in its stomach and gullet.

Occurrence of gorging

Very few squawfish were found with stomachs distended with food. The few taken in this condition were full of young salmon and were captured in close proximity to and within a few days following a release of artificially reared salmon. There were indications that the squawfish, under these conditions, were capable of "pumping" the undigested remains of salmon through the alimentary tract. Salmon remains were ejected from the anus when some of the squawfish were first handled. These remains even in the lower part of the intestinal tract showed little of the effect of digestion; the fins were whole and the integument intact.

Diurnal fluctuations in feeding

The sampling for data on diurnal fluctuations in the feeding activities of squawfish was inadequate. The majority of the catches were made at night, when gill-net fishing was most efficient, and the nets were usually lifted the following morning. The results from drift-net fishing, where the fish were captured during a relatively short period of time, were too meager to provide information on diurnal feeding.

Variation in feeding habits

Variations in the percentage occurrence of foods eaten by different-sized squawfish are shown in figure 5. In this illustration, the fish were grouped into 1-inch length classes and the percentage occurrences of the food items and empty stomachs were calculated and graphed. Due to duplication of food items in some stomachs, the summed percentages were, in most length classes, slightly more than 100 percent. However, since only 3 percent of the fish containing food contained more than one kind of food item, the highest total of summed percentages was only 105 percent. For clarity and simplicity in figures 5 and 9 none of these totals was plotted at more than 100 percent, so the area in the figures denoting the empty stomachs should be a bit more extensive. This slight loss of area in the empty category reduces only slightly the validity of the figure in presenting the relation between size and the occurrence of food items.

The most obvious change in food occurrences as the squawfish increase in size is the decrease in the occurrence of insect foods and the increase in

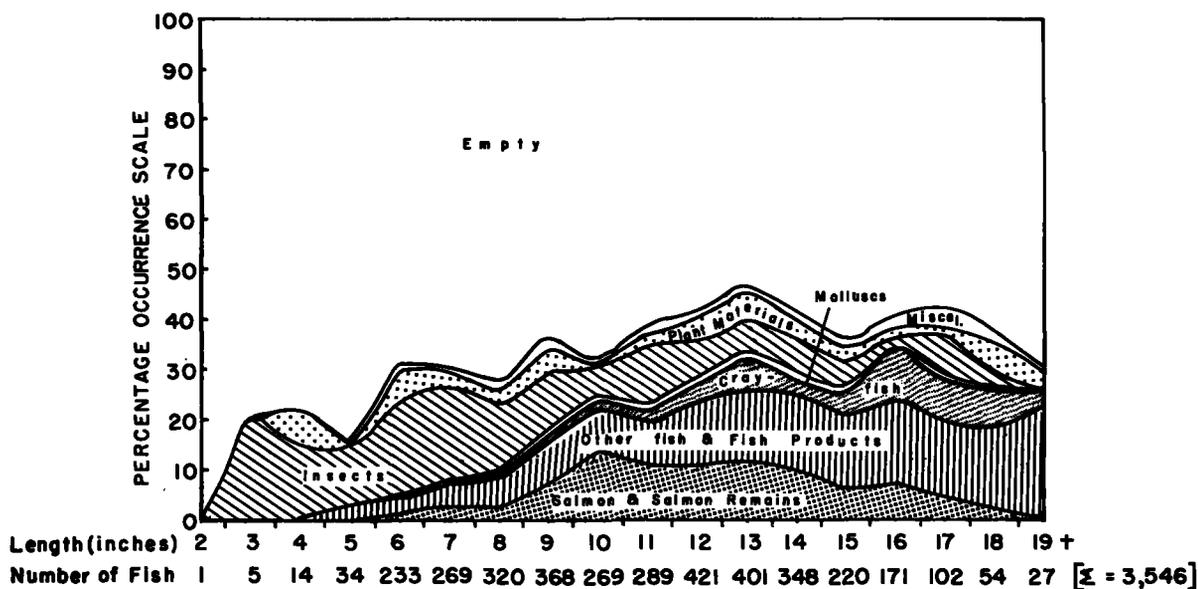


FIGURE 5.—Percentage occurrence of food items and empty stomachs by 1-inch length groups; sexes grouped.

occurrence of fish and crayfish. Other food items—mollusks, plant materials, and miscellaneous items—did not occur in great enough frequency to illustrate any trends. Plant materials were eaten equally often by all sizes of squawfish. Hynes (ibid.) observed similar changes in the size of food items in the diet of sticklebacks with a change in fish size and stated that the change “. . . is an expression of increase in maximum size of the organisms eaten.” Smaller fish are unable to swallow the larger organisms available to the larger squawfish, and as the fish grow larger it becomes less worth while to spend time catching the smaller food organisms.

The smallest squawfish found to have consumed salmon were 6 inches in total length (figs. 5 and 6). The length frequency of salmon-eating squawfish approximates the distribution of the total squawfish sample (fig. 6). The largest squawfish containing salmon was 18 inches in total length. Fish, including salmon, do not reach dominant occurrence in the stomachs until the squawfish are about 10 inches in total length (fig. 5). The percentage occurrence of fish then remains at approximately the 20-percent level. Insects decrease in occurrence markedly in squawfish of 9 inches total length, but are found in 2 to 10 percent of all larger fish. This evidence indicates that the most common food of the squawfish changes from insects to fishes at a total length

of 9 to 10 inches. (Preliminary age-length determinations indicate squawfish of this size to be approximately 4 years old.)

Ricker (1946) states that the larger fish have empty stomachs more often than do smaller ones, with few exceptions. Hynes' (ibid) stickleback data agree closely with Ricker's statement, and Hynes states, “It will be noted that as the fish grow the percent with empty stomachs increases steadily.” He interpreted this as indicating the sticklebacks eat more sporadically as they grow larger. Figures 5 and 7 indicate that for Lower Columbia River squawfish, the opposite situation is the general rule. Very few fish below 5 inches' total length were sampled, but a definite decrease is shown in the percentage occurrence of empty stomachs as the squawfish increase in size.

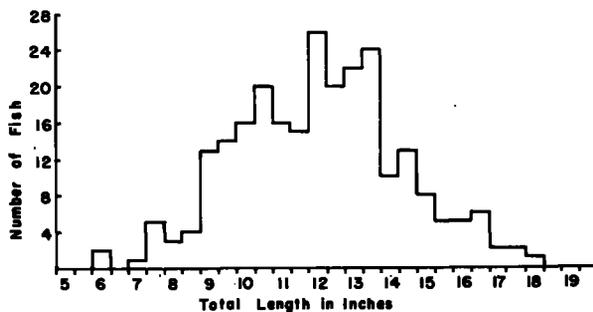


FIGURE 6.—Length-frequency distribution of salmon-eating squawfish.

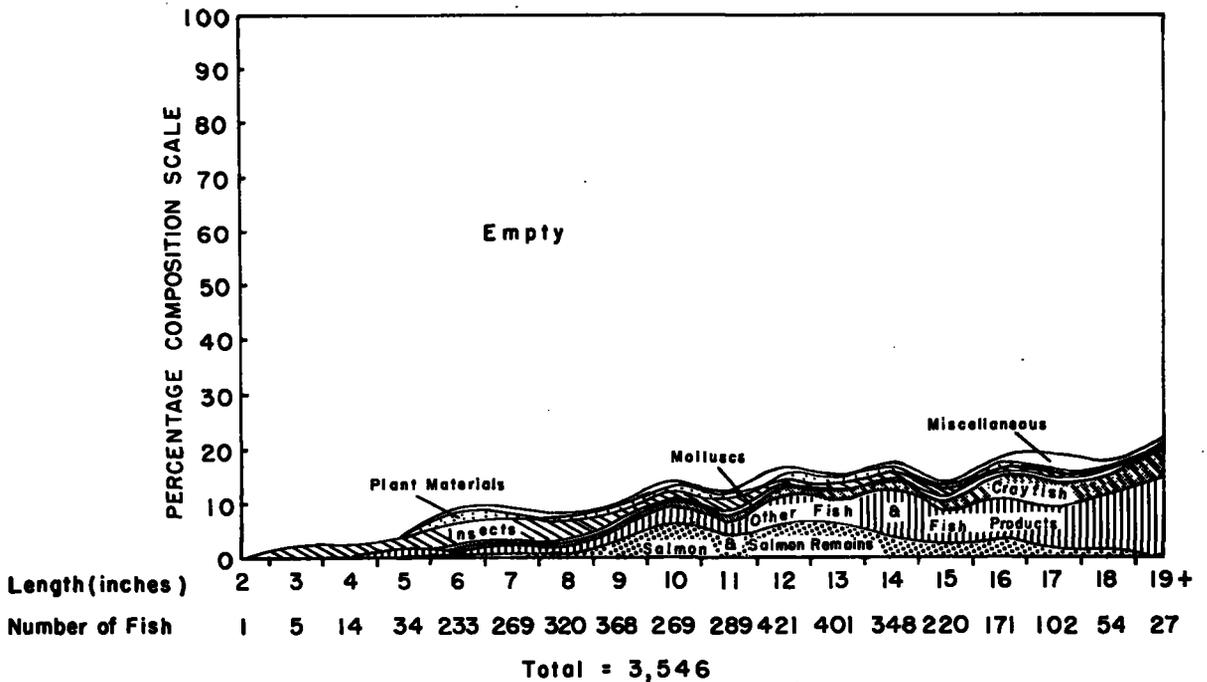


FIGURE 7.—Percentage composition of stomach contents of squawfish by 1-inch length classes.

The percentage composition of food items in relation to squawfish size (fig. 7) follows a pattern not unlike that of the percentage occurrence. Insects decrease in importance as the fish get larger and fishes and crayfish attain dominant importance in large fish. The point of transition in the importance of these categories also is at the 9- to 10-inch total length size. The lesser food items occur at about the same level of importance throughout the range of sizes, rarely comprising more than 2 percent of the stomach composition.

In comparing the frequency of occurrence (fig. 5) with percentage composition (fig. 7), two points of difference are readily apparent. The first is the increase in "emptiness" in the percentage composition. This is due to the occurrence of partially empty stomachs which were not included in the "empty" category of figure 5, but contributed points to that category when emptiness was considered as part of the composition of the stomachs. The second point is the decrease in comparative importance of the food items that are usually small, such as insects and plant materials. Salmon, other fishes and fish products, and crayfishes all seem to decrease in importance from figure 5 to figure 7, but the decrease in the smaller food items is proportionately much greater.

Variation by sex

Figure 8 shows the percentage composition of the stomach contents for the total sample for the categories of male, female, and the immature-unknown group. Slight differences are seen to occur in the diet of males and females, and, of

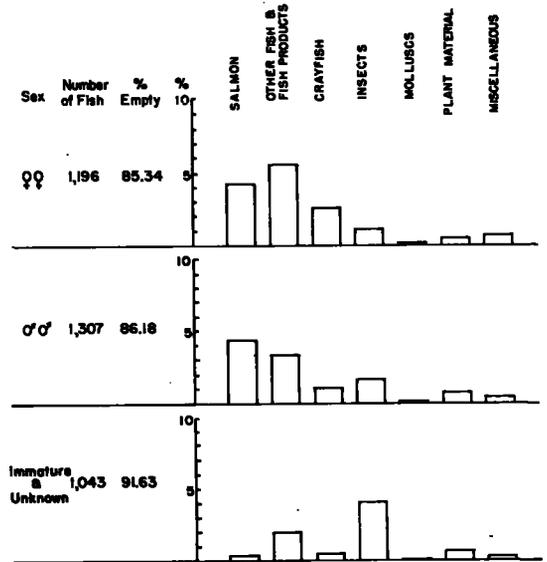


FIGURE 8.—Percentage composition of stomach contents for females, males, and the immature-unknown group.

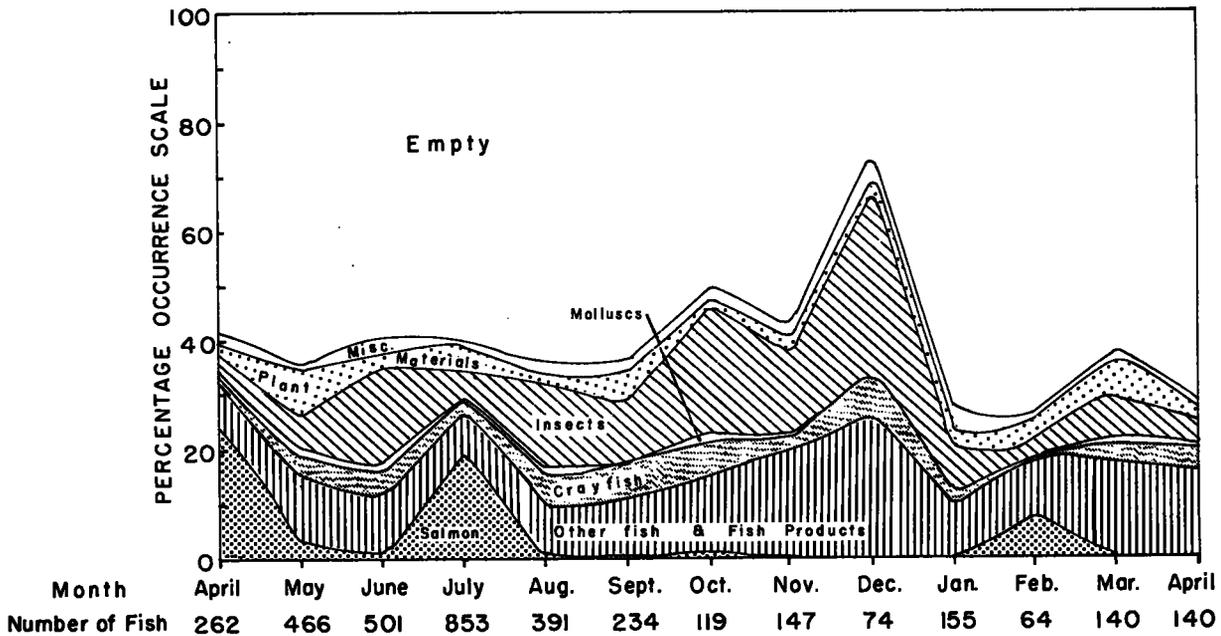


FIGURE 9.—Percentage occurrence of squawfish food items and empty stomachs, by months.

course, the diet of the immature fish is different due to their smaller size. However, the differences shown in figure 8 are within the limitations of the sampling and food evaluation techniques, neither of which were designed for detailed purposes. For this study, then, it is assumed that no differences exist in the feeding habits of male and female squawfish.

Variation by season

As would be expected in the feeding activity of coldblooded animals, there were distinct variations in the seasonal feeding activities and diet composition of the squawfish. The percentage of squawfish containing food held at a fairly constant level from April to November. A rise in food occurrence appeared in December, following which the percentage occurrence of stomachs containing food dropped to its lowest point in January (fig. 9). The percentage composition of the stomach contents (fig. 10) shows a similar pattern of seasonal variation.

The components of the diet also showed seasonal variations in quantity. Salmon were found to occur in significant amounts only following releases of young salmon from hatcheries where sampling occurred during and following releases in April, July, and February. Since it was not possible to sample for squawfish at every release of salmon

from all hatcheries in the Lower River, predation following releases during other months was missed. The occurrence of salmon in the squawfish diet appears to be dependent on hatchery releases, and is not associated with natural seasonal phenomena as are the other food items.

The other foods were found in usual occurrences and quantities except during the month of December, when the mean value of food points per stomach was unusually high (fig. 11). Closer examination of the December data indicates that the majority of the points were allotted to foods found in squawfish from Eagle Creek, Herman Creek, and the Wind River sites in the Bonneville Pool, and from Umatilla River, the uppermost tributary in which sampling occurred. The Bonneville Pool samples contained mostly nonsalmonoid fishes and a few insects. The Umatilla River December sample of 21 squawfish, none of which was empty, received 68 points for fish and 134 points for insects, the majority of the insects being stone-fly nymphs. The apparent increase in feeding activity in December is due, then, to results obtained from 74 stomachs, which were 2 percent of the total sample. These stomachs gained 507 food points for an average of 6.8 points per stomach, by far the highest average during any month.

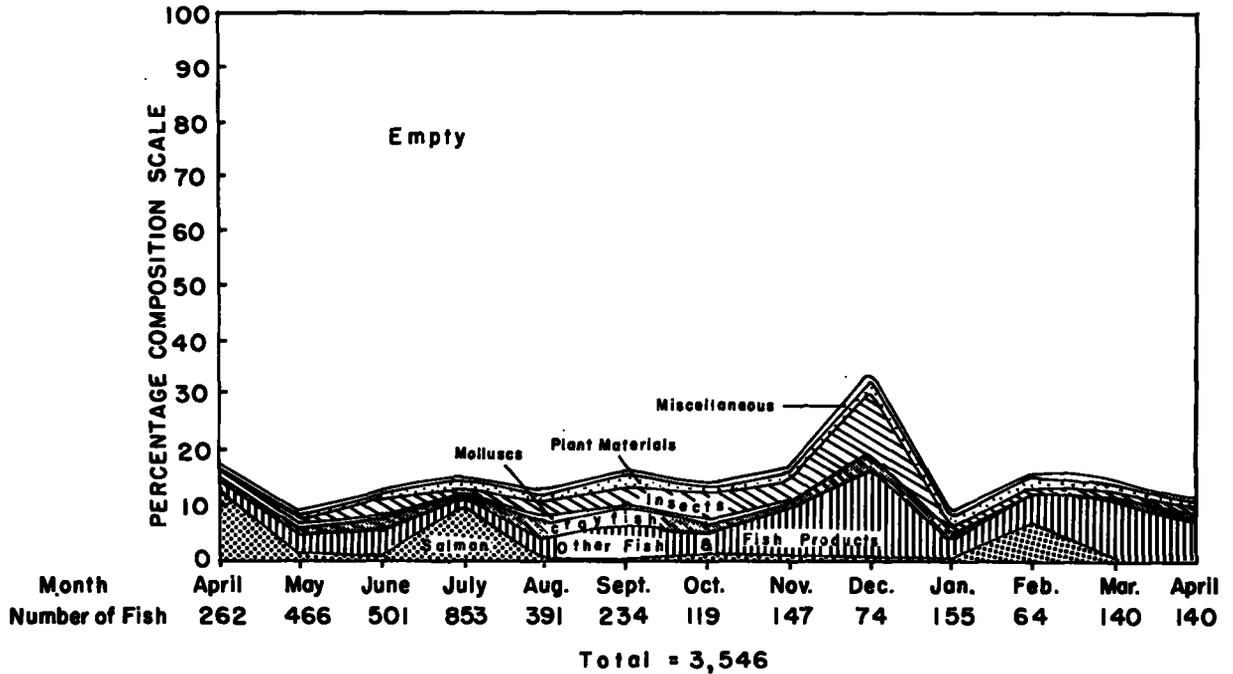


FIGURE 10.—Percentage composition of squawfish stomach contents, by months.

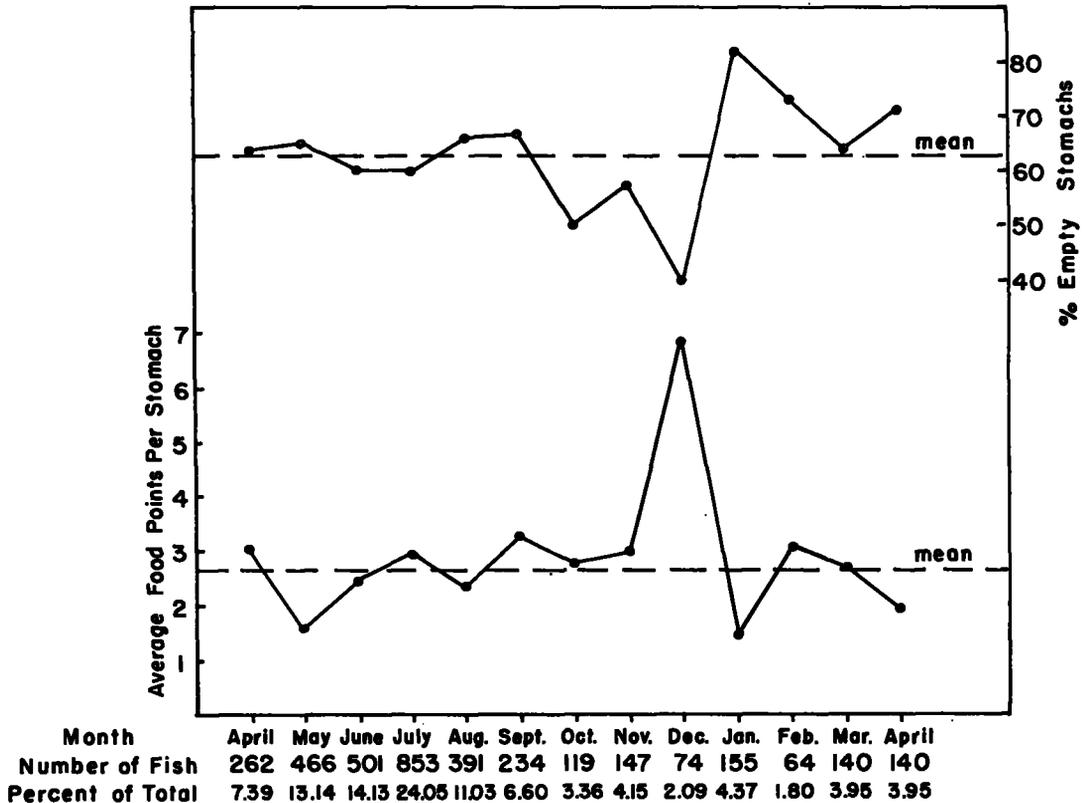


FIGURE 11.—Mean monthly food points and monthly percentages of squawfish with empty stomachs.

The mean monthly food points per stomach are shown in figure 11. The great variation between the annual mean and the December value of food points per stomach is readily apparent. Empty stomachs were at minimum percentages during the fall months, the minimum being December, concurrent with the peak in mean food points per stomach.

An explanation of the variation shown by the December samples is not readily available. The foods found do not differ in kind from those found during the remainder of the year, but the quantities do differ, not only from the adjacent months but from the whole year's sample.

Perhaps this is further evidence of the "opportunistic omnivorous" habits of the squawfish. They seem to feed to the gorging stage when desirable food items are available, but do not appear to hunt actively for food at all times. They are, it appears, a sluggish fish not willing to exert themselves in searching for food, but when an opportunity occurs, they are stimulated to feed voraciously and will do so until a point determined by capacity and availability is reached.

Variation by subarea

To determine whether or not the diet of the squawfish differed between subareas within the entire sampling area, the main area from Astoria to McNary Dam was divided into four smaller areas. The locations of these subareas and their boundaries are shown in figure 1 and described as follows:

Area I. Mouth of Columbia River to the mouth of the Cowlitz River, including the Cowlitz and its tributaries.

Area II. Mouth of the Cowlitz River to Bonneville Dam.

Area III. Bonneville Pool area; from the dam upstream to the site of The Dalles Dam.

Area IV. The Dalles Dam to McNary Dam. Collections for this study made only in the John Day and Umatilla Rivers in this subarea.

The percentage composition of foods for each area is shown in figure 12. Although the differences in foods between areas seem to be minor, chi-square tests indicated that differences for all food categories were significant. The variation in salmon occurrence and importance from one area to another is understandable in the light of the artificial factors contributing to salmon concentrations and abundances. The variations in

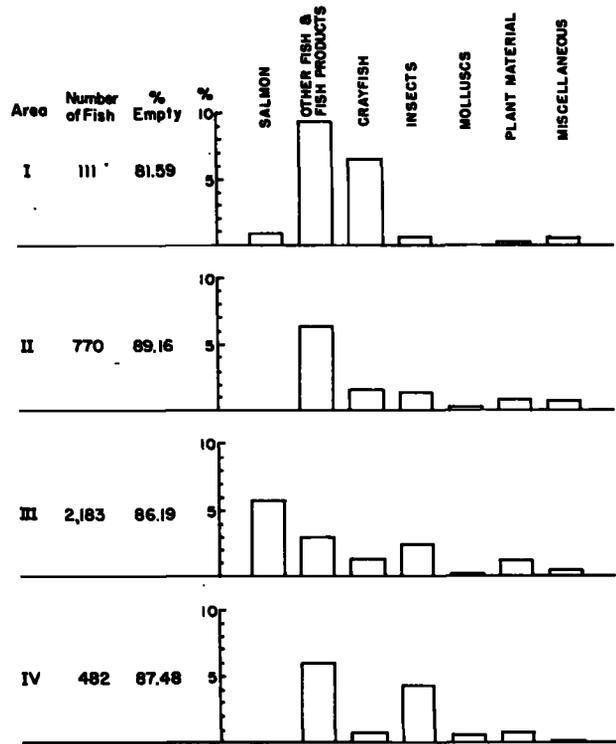


FIGURE 12.—Percentage composition of squawfish stomach contents from four subareas.

composition of other foods cannot easily be explained.

Since differences in food habits were found to be due in some measure to differences in size of squawfish, the length frequencies of the squawfish captured in each area were compared (fig. 13). The differences in size of squawfish between the subareas are difficult to compare because of differences in sample sizes. Inspection by eye indicates that the range of sizes was approximately the same in each area. The size composition of the samples from the different subareas, then, does not readily illustrate a reason for the food variations between areas. (Those fish smaller than 5 inches in area IV were taken with an electrical fish-shocking device.)

No faunistic sampling was made for the items of food found in the stomachs. Therefore, an estimate of the abundance of these food items in the subareas of the river cannot be made. An explanation of the area food differences may actually lie in differences in the abundance in food items and their availability to the squawfish.

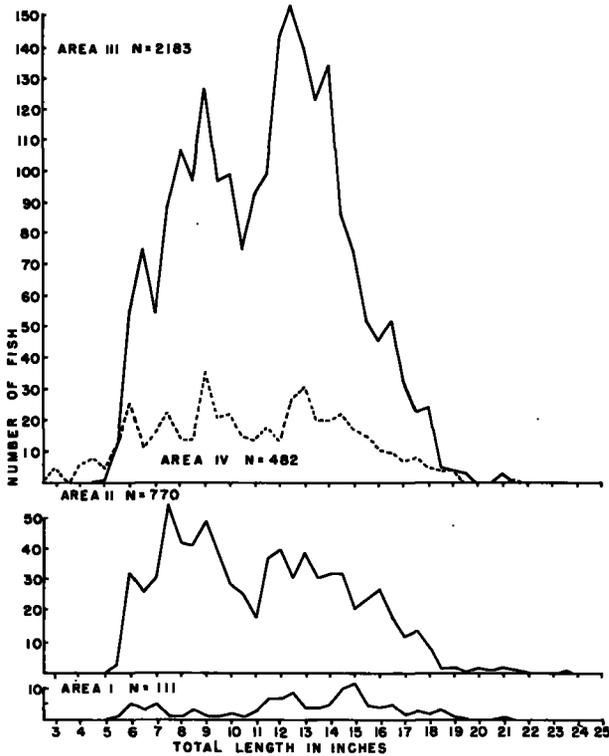


FIGURE 13.—Length-frequency distribution of squawfish by four subareas.

Further study on food item abundances and squawfish foods is necessary to attain an understanding of these area differences in squawfish foods.

A fact of importance emerging from the squawfish stomach analyses was the high occurrence of empty stomachs, particularly during the months of January, February, and March. Eighty-two percent of the January sample of 155 squawfish was completely empty. Another point of interest is that only 3 percent of the squawfish containing food contained more than one kind of food item.

Predation on juvenile salmon from hatcheries

From figure 14 it is readily apparent that every occurrence of salmon in squawfish stomachs was preceded by a recent and nearby release of artificially reared juvenile salmon. The predation noted in Germany Creek is the only exception. Most occurrences of salmon in stomachs were within a day or two following a release. Squawfish sampling was not continuous or intense enough within a sampling area to show a decrease

in the availability of salmon. The delays at the Wind River sites in the occurrence of salmon in squawfish stomachs following releases can be explained by the fact that the point of release at the Carson Hatchery is some 12 river-miles upstream from the sampling sites. There is a lagoon in the lower reaches of Wind River before it empties into the main Columbia River. The river distance would cause some straggling to occur in the salmon migration. A residual delay in the lagoon would also be a factor in the duration of availability of the young migrant salmon to the squawfish. The stream characteristics of Herman Creek could also allow some prolongation of availability of salmon to squawfish. The hatchery is located about one-half mile upstream, and there is also a small lagoon at the mouth of the creek.

Table 3 lists the gill-net sampling sites where squawfish were found which contained salmon fingerlings and also the nearest point of artificially reared salmon releases.

TABLE 3.—Sampling sites where salmon were found in squawfish, and nearest source of hatchery-released salmon

Site	Nearest hatchery and location
Germany Creek	None close by.
Herman Creek	Ox Bow Hatchery (Oregon Fish Commission) approximately $\frac{1}{4}$ mile of stream and $\frac{1}{4}$ mile of "estuary" above net site.
Wind River Mouth and Upper Wind River.	Carson Hatchery (U.S. Fish and Wildlife Service), about 14 miles above mouth of river and about 12 miles above Upper Wind River site.
Drano Lake	Little White Salmon Fish Cultural Station (U.S. FWS), at mouth of Little White Salmon River where it enters Drano Lake.
Drinking Fountain	Willard Hatchery (U.S. FWS), about 6 miles upstream from mouth of Little White Salmon River.
Spring Creek	Spring Creek Fish Cultural Station (U.S. FWS) about $1\frac{1}{2}$ miles upstream from gill net site.
	Spring Creek Fish Cultural Station (U.S. FWS). One net site was in front of hatchery and another one about 150 yards downstream.

SUMMARY AND CONCLUSIONS

(1) This study is based on the examination and evaluation of the stomach contents of 3,546 squawfish collected during the 13-month period of sampling from April 1955 to April 1956, from the lower 240 miles of the Columbia River and its major tributaries within this area.

(2) The evaluation of the foods is presented numerically for the identifiable fishes, and by percentage occurrence and percentage composition for all foods. The percentage composition is based on a modification of a "point" system of food assessment.

(7) Slight differences were found to occur in the diets of male and female squawfish. However, these differences were not considered significant enough to warrant the separation of the sexes in the food study, and the results of analysis of stomach contents of males and females were grouped.

(8) Some variations in diet due to seasons of the year were noted, but could not be explained completely. Most food items were found during all seasons. Fishes, other than salmon, and crayfish had no definite period of scarcity or abundance in the squawfish diet. Insects were at their minimum in the stomachs during the first calendar quarter. The period of maximum insect occurrence was from August to December.

(9) Some differences in diet between subareas of the main sampling area were evident. Complete understanding of the reasons for this must await further study aimed at this particular problem. The food item showing the greatest variation from one area to another was salmon, the area distribution of which was considered the result of artificial propagation and release.

(10) The most striking and obvious result of this study was the detection of the localization of predation on hatchery-released salmon to the immediate vicinity of the release points. It is recommended that future studies be conducted to measure the absolute effect of such predation; that is, to determine the total losses of released salmon to predators within a given distance of the point of release. Such a program of study would be far from simple, but should be initiated soon in consideration of the large financial expenditures necessary to produce these young salmon, justified at present only by the expectation that they survive to provide a significant contribution to the commercial fishery.

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FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

EFFECTS OF FERTILIZING BARE LAKE, ALASKA, ON GROWTH AND PRODUCTION OF RED SALMON (*O. NERKA*)

By PHILIP R. NELSON



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ABSTRACT

Bare Lake, a 120-acre, unstratified lake on Kodiak Island, Alaska, was fertilized each year from 1950 to 1956 with inorganic fertilizers to determine whether fertilization will increase production of red salmon (*Oncorhynchus nerka*). Various phases of the life history of the species were studied.

From 1950 through 1956 the annual spawning population of red salmon in Bare Lake ranged from 52 to 551 fish. Red salmon vary in age at maturity. The majority of Bare Lake red salmon remain in the lake slightly longer than a year, then migrate to the sea to spend 3 years before returning to the lake to spawn. Females predominated over males in the spawning escapement each year. Data are presented on fecundity, egg retention, and the annual egg deposition.

A relation was found between the growth of young red salmon and the gross rate of photosynthesis. Fertilization has brought about an increase in size of the seaward-migrating red salmon smolts. There is good evidence to show that the larger smolts survive in greater numbers at sea. For the years 1950-53, fresh-water survival has ranged from 1.0 to 5.1 percent and marine survival increased from 3.3 to 7.9 percent. Limited information is available on the effect of fertilization on other fish populations in Bare Lake.

EFFECTS OF FERTILIZING BARE LAKE, ALASKA, ON GROWTH AND PRODUCTION OF RED SALMON (*O. NERKA*)

By PHILIP R. NELSON, *Fishery Research Biologist*
BUREAU OF COMMERCIAL FISHERIES

Bare Lake, on Kodiak Island, Alaska, was fertilized each year for 7 years, from 1950 to 1956. The limnological effects of fertilizing the lake were described by Nelson and Edmondson (1955). The present paper deals primarily with the effects of fertilization on the red salmon population and briefly with the effect on other fish populations in Bare Lake.

Fertilization experiments were initiated at Bare Lake on the basis of studies conducted earlier at Karluk Lake, which is only 15 miles from Bare Lake. The hypothesis upon which the fertilization experiments were based was discussed by Nelson and Edmondson (1955). Briefly, it was proposed by these investigators that the decline in the Karluk River salmon runs may have resulted from a decline in the productivity of the lake waters. The carcasses of spawned salmon in the earlier years, when the escapements were large, contributed a great amount of nutrients to the lake water. In recent years, with small escapements, the amount of nutrients furnished has been considerably less. It was hypothesized that by the addition of inorganic fertilizer the earlier productive capacity of Karluk Lake might be restored. Rounsefell (1958) cites other hypotheses as possible reasons for the decline in the Karluk River red salmon runs in his comprehensive report on Karluk Lake. It is recognized that many other factors, including meteorological conditions, diseases, and predator and competitor fishes influence the survival and growth of red salmon. The effects of these factors on the production of red salmon at Bare Lake were considered.

In this study, Bare Lake was fertilized to determine if this process would bring about an increase in fish food so as to augment red salmon

production. Bare Lake (fig. 1) was selected for this study because it has a run of red salmon; it is located close to the major red salmon producing lakes in the area; and, because of its small size (120 acres), the costs of experimentation would not be excessive and the results of fertilization could be more accurately determined.

For fertilization to be a useful management tool, not only must production of fish be increased but the costs must be economically justifiable. At Bare Lake, nitrate and phosphate fertilizers were added each summer in amounts necessary to increase the nitrate concentration approximately 0.25 milligram per liter, and the phosphate concentration 0.05 milligram per liter. In 1950 and 1951, the lake was fertilized just prior to mid-July. During the years 1952 to 1956, fertilizer was added in two lots during the first half of the months of June and July. The concentration achieved on each addition was one-half the amount specified. Choice of the amount was based on a prognostic experiment conducted during 1949 in which jugs of water were fertilized with varying concentrations of nitrate and phosphate and the rates of photosynthesis and of phyto-



FIGURE 1.— Aerial photograph of Bare Lake.

plankton growth measured (Nelson and Edmondson, 1955).

The fertilizers most frequently used were sodium nitrate and ammonium monohydrogen orthophosphate. The application consisted of mixing the fertilizers on a raft and subsequently using brooms to sweep the mixture into the water as the raft was towed about the lake. Usually the mixture was applied to the littoral zone, but on two occasions it was spread over the entire lake. No significant difference was found between the two methods in the concentration achieved in the lake water. The annual cost of fertilizers averaged less than \$400.

Numerous lake fertilization studies have been conducted by other investigators with the objective of increasing fish growth or survival. The lakes fertilized have differed widely in their characteristics and the amount and types of nutrients introduced have varied considerably. Lakes are extremely dissimilar in productive capacity and until more is learned of the extent to which various factors govern productivity, fertilization programs will continue to be exploratory.

Good bibliographies and reviews of fertilization studies are presented by Mortimer and Hickling (1954) and Maciolek (1954). Maciolek reports that "Conclusions drawn from all lake-fertilization trials indicate that fish may have benefited from enrichment in only three experiments." Fortunately, much has been learned even from the unsuccessful attempts to aid workers in future studies.

Since these reviews, Weatherley and Nicholls (1955) reported on the results of fertilizing a small, shallow Tasmanian highland lake. The added nutrients stimulated growth of aquatic plankton and epiphytic fauna which created a marked increase in the growth of trout.

Fertilization experiments had been confined to rather small lakes until Eguchi and others (1954) reported the enrichment of Lake Skikotsu in Hokkaido. This lake has an area of 75 square kilometers and a mean depth of 265 meters. It was enriched in May 1953 with the objective of increasing the size of landlocked red salmon. Since fertilization of the lake, an increase in plankton abundance has occurred, but as yet no report has been given on the effect on fish populations.

In fertilization studies a constant danger exists of overfertilizing. In such instances vast amounts of blue-green algae usually appear and eventually upon decomposition of the algae an anaerobic condition develops in stratified lakes or, during winter, in lakes covered by ice. This happens not only in fertilization experiments (Ball 1950; Ball and Tanner, 1951), but lakes often have been rendered excessively productive by large introductions of domestic sewage. A recent example of the latter is reported by Edmondson, Anderson, and Peterson (1956) to be taking place in Lake Washington at Seattle, Washington. At present we have observed no indications of overfertilization at Bare Lake. A winter trip in February 1955 showed a plentiful supply of oxygen at all depths except immediately over the bottom, and other symptoms of overfertilization have not appeared.

Following the last fertilization of Bare Lake in 1956, limited studies were planned in subsequent years to provide a comparison of conditions in the lake and red salmon production during and after fertilization. At the time of this writing it was too early in the investigation to ascertain the full effects of fertilization on fresh-water survival of salmon; nevertheless, some interesting effects have been found in regard to the fresh-water growth and marine survival of red salmon.

The primary purpose of this study was to determine whether fertilization will substantially increase red salmon production. If the method is successful, it might prove useful for increasing red salmon production in other red salmon lakes. It also was necessary to study most phases of the life history of the Bare Lake red salmon. The first section of the paper deals with characteristics of the adult population, while the latter sections show the effect fertilization has had on the growth and survival of the species.

Many have contributed to the studies at Bare Lake. Men of the United Fishermen of Alaska helped support the work financially. Field workers who contributed materially to the collection of data were Carl E. Abegglen, Robert C. Davison, Charles J. Hunter, Clark S. Thompson, Carl R. Schroeder, Alfred J. Schroeder, Ralph L. Swan, Robert T. Heg, Charles W. Huver, Robert Raleigh, Jerry Larrance, and Paul H. Hatch. W. T. Edmondson assisted in the limnological

analysis and reviewed the manuscript. Advice on statistical analyses was given by members of the Biometrics Unit, Pacific Salmon Investigations.

ADULT RED SALMON POPULATIONS OF BARE LAKE, 1950-56

ANNUAL ESCAPEMENT AND RUN

All that is known of the history of the Bare Lake red salmon population has been obtained from scattered reports of a few men who visited the lake before 1949. About the only information available was that some red salmon spawned in the lake; no surveys or counts had been recorded of the numbers of fish present.

The present study was commenced in 1949, when observations on the spawning escapement into the lake, estimated at 300 fish, were made by airplane. Because of the many errors involved in measuring fish populations by aerial observation, the accuracy of this figure is questionable. Subsequently, a trap for salmon has been maintained each year of the study on Bare Creek, the outlet stream. The trap was located about 50 feet downstream from the outlet, where the creek is 6½ feet wide. At the lower (downstream) end of the trap a picket fence was constructed with an upstream lead in it. About 10 feet farther upstream another picket fence was placed across the stream to block the passage of adult salmon. Fish migrating upstream were led into the trap and were easily captured in the shallow water. A section of the trap bottom was deepened to provide a suitable resting place

for the fish. The smolt trap was placed immediately upstream from the adult trap. This trap consisted of an 18-gauge, 6-mesh-to-the-inch screen placed across the stream to block the downstream movement of smolts. Above this was a V-shaped lead constructed of mesh of the same size. A diagram of the weir structures is shown in figure 2.

Daily, all adult salmon entering the trap were removed by dip net. The fish were measured, a scale sample was taken for age determination and the sex recorded. The fish were then released into Bare Creek above the trapping area. The annual count of salmon released into Bare Lake from 1950 to 1956 is shown in table 1; not included in these data are a few salmon taken for fecundity studies. The escapements ranged from 52 to 551 red salmon with an annual mean of 319 during the 7-year period. The bulk of the escapement appeared at the weir from mid-June

TABLE 1.—Weekly escapement of red salmon into Bare Lake 1950 to 1956

Week ending	1950	1951	1952	1953	1954	1955	1956
May 24.....					2		
31.....					1	5	2
June 7.....	8			16	1	7	8
14.....	18	4	45	5	26	20	40
21.....	200	20	130	97	113	137	98
28.....	76	21	64	103	10	85	108
July 5.....	90	3	28	27	49	139	57
12.....	150	3	110		15	9	26
19.....	2	1		1		12	6
26.....	6		2		3	2	
Aug. 2.....			1		13	1	1
9.....			1			1	1
16.....	1						1
23.....							
30.....				1		2	
Sept. 6.....			1				
Total.....	551	52	382	250	232	420	347

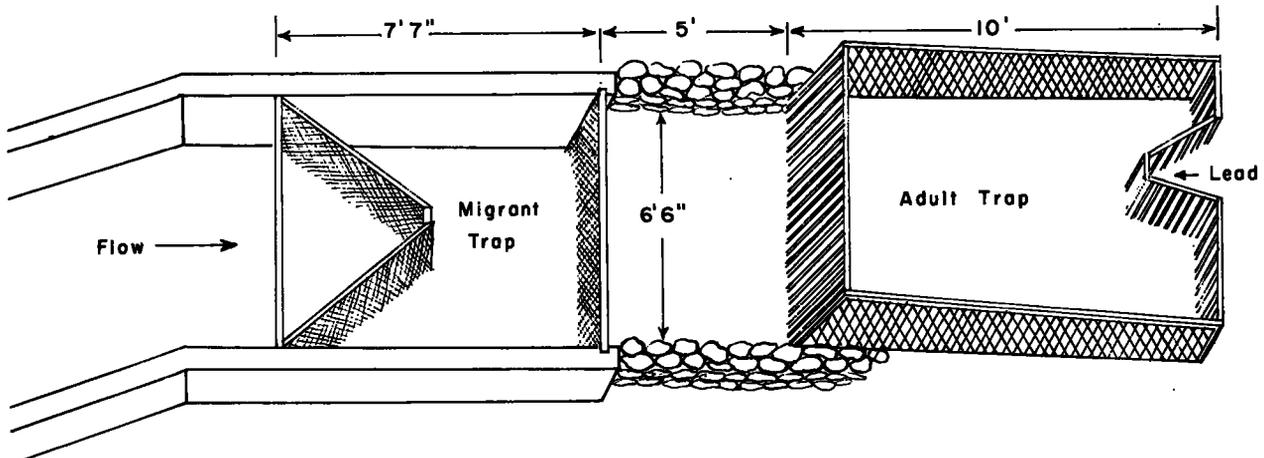


FIGURE 2.—Diagram of smolt and adult salmon traps placed across Bare Creek.

to mid-July. In 6 of the 7 years, the median of the escapement occurred during the week ending June 28.

There seems to be a tendency for the years with the largest total escapement, namely 1950, 1952, and 1955, to have two distinct peaks of abundance. For these years one peak occurred during the week ending June 21, and the other peak appeared 3 weeks later in 1950 and 1952 and 2 weeks later in 1955. The 4 years of small escapements show one prominent peak of abundance, and 1953 and 1954 each had a low subsidiary peak. Some Bare Lake fish are taken in the fishery; however, upon combining the escapement and catch, the peaks of abundance were

unchanged. It is not known at present whether fish occurring during these two peak periods represent distinct populations, or if they are parts of a common population.

To determine the annual Bare Lake run (catch plus escapement), it was necessary to determine the number of Bare Lake fish taken in the commercial fishery of the Red River district. Since Bare Creek is a tributary of the much larger Red River it is believed the fishery in the district removes a proportional amount of fish from the two runs. A map of Kodiak Island (fig. 3) is presented to show the location of Red River, Bare Lake, and the fishing district which extends along the coast from the mouth of Red River

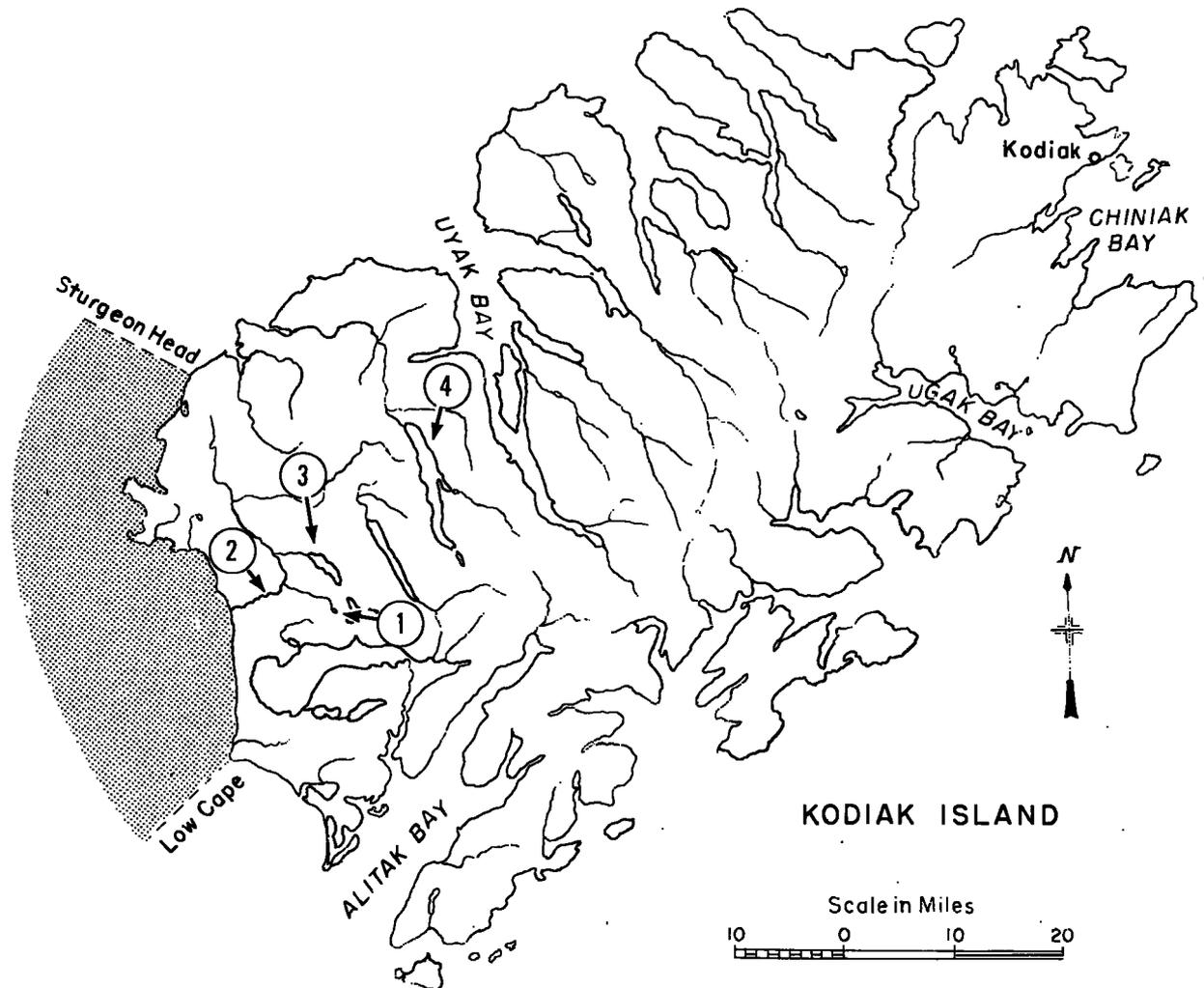


FIGURE 3.—Kodiak Island, Alaska. Shaded areas indicate Red River fishing district. (1) Bare Lake; (2) Red River; (3) Red Lake; (4) Karluk Lake.

approximately 30 miles north to Sturgeon Head and about 15 miles south to Low Cape. All fish captured in the fishing district are assigned to the Red River run of which Bare Lake is a part. Of the total run in the district, the Bare Lake run comprises less than 1 percent.

Annually a count is made of the number of red salmon entering Red Lake by means of a weir situated immediately downstream from the lake outlet. Tagging of red salmon at the mouth of Red River by fishery-management biologists indicates the fish spend approximately 1 week en route from the sea to the weir. Travel time to Bare Lake, although not determined, is estimated to be 1 week also, since the distances involved are about the same for both runs. To relate the occurrence of the escapement to the time of the catch, weekly escapement records were set back 1 week. Thus, escapement figures for Bare and Red Lakes were standardized to the time the fish appeared in the fishery. Hence, during periods of fishing it was possible to calculate for Red River what percentage the catch was of the escapement. This percentage was then applied to weekly escapement figures at Bare Lake to determine the catch of Bare Lake salmon (table 2). It is assumed in this calculation that the ratio of escapement to catch is the same for Bare Lake and Red Lake. In table 2, the weekly escapement and catch were added to show the weekly run of fish to Bare Lake. The weekly runs were then summed to provide the annual run.

TABLE 2.—Calculated Bare Creek red salmon run
[Based on catch-escapement ratios of the Red River run]

Week ending	Red River ¹			Bare Lake		
	Es- cape- ment ²	Catch	Ratio of catch to escapement	Es- cape- ment ³	Calcu- lated catch	Run ⁴
1950						
June 7	800					
14	4,800					
21	9,300	3,100	33 percent			
28	1,700					
July 5	17,200					
12	600					
19	800					
26	6,200	1,100	109 percent			
Aug. 2	400	6,100				
30						
Total						
1953						
May 31	500					
June 7	10,100					
14	8,100					
21	27,900	16,000	56 percent			
28	(*) 2,500					
July 5	14,400	3,000				
12	13,800	9,800				
Aug. 23						
Total						
1954						
May 17						
24						
31						
June 7						
14	33,900					
21	800	1,800	225 percent			
28	27,100					
July 5	400					
12	500	300				
19	14,300	12,800	74 percent			
26	11,400	3,500				
Aug. 2	900	3,500				
Total						
1955						
May 24						
31						
June 7	2,900					
14	10,300					
21	10,800					
28	28,500					
July 5	9,100					
12	9,200	300				
19	8,000	1,100	22 percent			
26	100	1,600				
Aug. 2	100	900				
23						
Total						
1956						
May 24						
31						
June 7	200					
14	9,200					
21	21,300					
28	13,800					
July 5	2,100					
12	10,900	4,700				
19	11,600	11,600	204 percent			
26	3,300	3,800				
Aug. 2	100	10,800				
9	2,800	3,900				
Total						

TABLE 2.—Calculated Bare Creek red salmon run—Con.
[Based on catch-escapement ratios of the Red River run]

Week ending	Red River ¹			Bare Lake		
	Es- cape- ment ²	Catch	Ratio of catch to escapement	Es- cape- ment ³	Calcu- lated catch	Run ⁴
1952						
June 7	800			45		45
14	4,800			132		132
21	9,300	3,100	33 percent	64	21	85
28	1,700			35		35
July 5	17,200			114		114
12	600			2		2
19	800			2		2
26	6,200	1,100	109 percent	1	1	2
Aug. 2	400	6,100		1	1	2
30				1		1
Total				397	23	420
1953						
May 31	500			16		16
June 7	10,100			5		5
14	8,100			101		101
21	27,900	16,000	56 percent	108	60	168
28	(*) 2,500			27	15	42
July 5	14,400	3,000				
12	13,800	9,800		1	1	2
Aug. 23				1		1
Total				250	76	335
1954						
May 17				2		2
24						
31				1		1
June 7				27		27
14	33,900			118		118
21	800	1,800	225 percent	10	22	32
28	27,100			51		51
July 5	400			15		15
12	500	300		3		3
19	14,300	12,800	74 percent	13	2	15
26	11,400	3,500		13	10	23
Aug. 2	900	3,500		1	1	2
Total				241	35	276
1955						
May 24				5		5
31				7		7
June 7	2,900			20		20
14	10,300			142		142
21	10,800			38		38
28	28,500			144		144
July 5	9,100			12		12
12	9,200	300		12	3	15
19	8,000	1,100	22 percent	3	1	4
26	100	1,600		1		1
Aug. 2	100	900		1		1
23				2		2
Total				437	4	441
1956						
May 24				2		2
31				8		8
June 7	200			41		41
14	9,200			98		98
21	21,300			108		108
28	13,800			58		58
July 5	2,100			26		26
12	10,900	4,700		7	14	21
19	11,600	11,600	204 percent			
26	3,300	3,800		1	2	3
Aug. 2	100	10,800		1	2	3
9	2,800	3,900		1	2	3
Total				350	18	368

¹ Red River escapement and catch figures rounded to nearest 100 salmon.

² The Red Lake escapement was set back 7 days to coincide with the time salmon were taken in the catch.

³ The Bare Lake escapement, including salmon mortalities at the weir plus fecundity samples, was set back 7 days to coincide with the time salmon were taken in the catch.

⁴ Catch plus escapement. ⁵ Estimated escapement. ⁶ Less than 50.

The calculated catch of Bare Lake red salmon exceeded the escapement approximately twofold in 1951, and amounted to about 60 percent of

the escapement in 1950 and 30 percent of the escapement in 1953. For the years 1952, 1954, 1955, and 1956, the catch ranged from less than 1 percent to 15 percent of the escapement. Low percentages of Bare Lake fish taken in the fishery those years were brought about by regulations which prohibited any fishing of the early Red River run. Since Bare Lake fish appear in greatest numbers early in the season, the majority escaped the fishery.

AGE COMPOSITION

Each year of the study, with the exception of 1950, scale samples were taken from all adult fish that entered Bare Lake. In the 1950 season, scales were taken from more than half of the fish in the escapement, and the weekly age composition was based on the age composition of the samples taken. Nine age groups¹ of adult salmon have been noted at Bare Lake: 3₂, 4₁, 4₂, 5₂, 5₃, 6₃, 6₄, 7₃, and 7₄. Of these, only three age groups are of major importance to the escapement, 5₂, 6₃, and 5₃, in decreasing order of importance.

The weekly percentage occurrence of each age group in the escapement has been calculated for each year (table 3). During the years 1950 through 1953, the 5₂ age group predominated, while fish of the 6₃ age group were most abundant in subsequent years. The predominance of one age group over the other is dependent on the percentage age composition of 2- and 3-year-old smolts 3 years before the escapement. A tendency exists for fish in the 6₃ age group to return early in the season. As shown in table 3, in 5 years out of 7 high percentages of this age group occurred early in the season and declined as the season progressed. Gilbert and Rich (1927) noted a similar characteristic in red salmon of this age group at Karluk Lake.

¹ The method, first used by Gilbert and Rich (1927) to designate the age of red salmon, is as follows: A fish resulting from an egg laid in the spawning gravels in 1950 and that migrated to the ocean in 1952 and returned to the river in 1955 is called a five-two and designated thus, 5₂. Such a fish would have emerged from the gravels of the spawning beds in the spring of 1951 and would have spent 1 growing season or summer in fresh water. In referring to its fresh-water history it is called a two-fresh-water fish because it migrated seaward in its second year. It would have spent 3 full growing seasons, i.e., 1952, 1953, 1954, and part of a fourth year in the ocean; but in referring to its ocean history it is called a three-ocean fish, because it returned as an adult in the third year following its seaward migration. A fish that migrated to the ocean in its third year and returned in its sixth is called a six-three and is designated 6₃.

TABLE 3.—Weekly percentage occurrence of red salmon, by age group, in the Bare Lake escapement, 1950 to 1956

Year	Percentage occurrence in age groups—								
	3 ₂	4 ₁	4 ₂	5 ₂	5 ₃	6 ₃	6 ₄	7 ₃	7 ₄
1950									
June 7				75		25			
14				84		6			
21				94	1	5			
28				95		5			
July 5				94		6			
12				91	5				4
19				100					
26 ¹				100					
1951									
June 7				75	25				
14				50	5	35			5
21			9	76	5	10			
28				67		33			
July 5				25	50	25			
12									
19				100					
1952									
June 7				69	7	22			
14			2	58	7	32			
21		1	2	74	5	16			
28		2	3	37	20	40			
July 5			3	74	6	15			
12			5	87		13			
19									
1955									
June 7				69	6	25			
14				80		20			
21			1	79	14	6			
28			1	89	14	3			
July 5			3	93	4				
12									
19				100					
1954									
May 31						100			
June 7						100			
14				8	4	15			
21			1	10	5	24			
28					10	40			
July 5				4	6	47		2	
12				33	13	27			
19									
26				33	67				
Aug. 2				8	61	31			
1953									
May 31				40	20	40			
June 7				43		57			
14				20	15	60			5
21				40	20	38			
28			2	33	22	43			1
July 5			1	44	20	32			
12			4	33	42	17			
19			8	42	8	50			
26				33	33				
Aug. 2		33		33	33				
2		25		50	25				
1956									
May 31						100			
June 7				25	13	62			
14				20	24	56			
21				28	14	55			
28			3	30	17	43			
July 5			8	29	14	53			2
12				29	14	53		2	2
19			4	15	81	81			
19 ¹				50	12	38			

¹ Added to the escapement for this week are a few red salmon which entered the lake after this date. The number of red salmon involved are as follows: 1 in 1950, 5 in 1952, 1 in 1953, 3 in 1955, and 2 in 1956.

The annual age composition of the Bare Lake run and the number of salmon in each age group were determined by calculating the number of fish in the weekly run (table 2) that fell in the various age groups (table 3). The weekly totals for each age group were combined to give the total number of fish in each group and percentage

TABLE 4.—Age composition of the red salmon run at Bare Lake, Alaska
[Percentage in parentheses]

Year	Number in run	Number and percentage in age group—								
		3 ₂	4 ₁	4 ₂	5 ₂	5 ₃	6 ₃	6 ₄	7 ₃	7 ₄
1950.....	943				880 (93.3)	16 (1.7)	37 (3.9)			10 (1.1)
1951.....	167		6 (3.6)	3 (1.8)	104 (62.3)	15 (9.0)	36 (21.5)			3 (1.8)
1952.....	420		3 (0.7)	13 (3.1)	276 (65.7)	30 (7.2)	98 (23.3)			
1953.....	335		3 (0.9)	4 (1.2)	271 (80.9)	41 (12.2)	16 (4.8)			
1954.....	276		1 (0.4)	23 (8.3)	17 (6.2)	92 (33.3)	142 (51.4)	1 (0.4)		
1955.....	441	2 (0.5)		12 (2.7)	172 (39.0)	87 (19.7)	166 (37.6)			2 (0.5)
1956.....	368			13 (3.5)	104 (28.3)	54 (14.7)	193 (52.4)		1 (0.3)	3 (0.8)

age composition of the run each year (table 4). In this calculation it is assumed that the age composition of the escapement reflects the age composition of the run. If it were possible to distinguish Bare Lake fish in the catch, it might be found that this was not true in 1950 and 1951, the years of large catches. Since then the calculated catches have been small and probably have had little influence on the age composition of the escapement.

With knowledge of the size and age composition of the annual runs, the return of salmon from known spawning escapements or smolt migrations can be measured.

LENGTHS

In the process of taking scales of adult salmon at the weir, the sex and fork length of each fish were recorded. In figure 4, the mean fork length by sex for fish of each ocean age is presented for each year. As insufficient numbers of 2-year-old ocean-age fish were present in samples for 1950, this group has been omitted. It is quite apparent from the figure that the size of the adults is dependent on the years spent in the sea and the sex of the fish. In fact, the criteria affecting ocean growth apply to both sexes and to both ocean ages. Indications of this were recorded by Gilbert (1915) for red salmon in British Columbia and have been reported since from other areas. The good relation in size each year between 2- and 3-year-old ocean-age fish of both sexes would suggest that environmental factors in the ocean, probably during the last year, have the greatest influence in determining size at maturity.

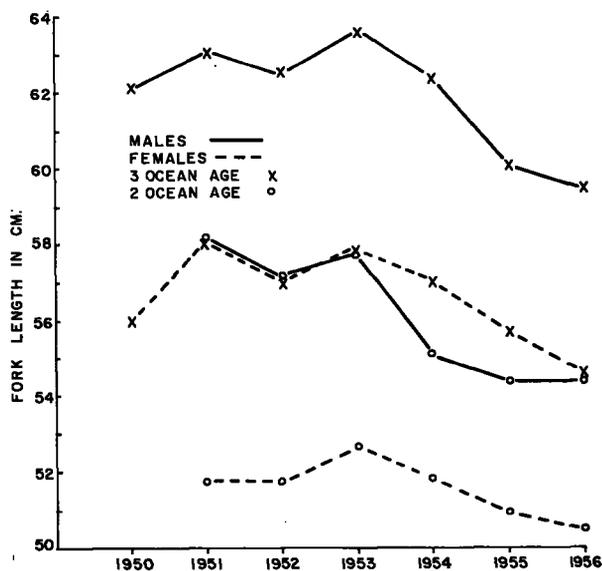


FIGURE 4.—Mean fork length of red salmon in the escapement, by sex and ocean age.

No significant difference in the size of adults of the same ocean age but of different fresh-water ages was found. Over the years, the average percentage increase in length of fish spending an additional year in the ocean was 9.2 for both sexes. At the same time, males averaged 8.2 percent longer than the females. On the basis of female red salmon taken for fecundity samples at the weir (appendix table 1), the average weight of 2-year-old ocean fish was 3.68 pounds, while 3-year-old ocean fish averaged 4.78 pounds. Although the 3-year-old ocean females averaged 9.2 percent longer than the 2-year-old ocean females, the increase in weight was 23 percent. Weights of adult males have not been taken, but

it is probable that a similar weight relation exists between 2- and 3-year old ocean males.

SEX RATIOS

Sex ratios were established by examining live fish in a holding box at the weir site. Although it was possible to examine the fish rather carefully, some errors are made in sexing live fish, especially when the spawning characteristics of fish of each sex are only partially developed. For example, in 1953, spawning-ground recoveries were made of 901 live red salmon, sexed at the Karluk River lagoon (Nelson and Abegglen, 1955). The fish were placed in a holding box and sexed by superficial examination before being tagged. Later, on the spawning grounds the tagged fish were recovered dead and at that time the sex could be accurately determined by dissection. It was found that 5 percent of the live fish were sexed incorrectly; however, there was no tendency to sex incorrectly a greater proportion of fish of one sex than the other (Fish and Wildlife Service, unpublished data). Similarly, at Bare Lake, during the 4 years that recoveries on the spawning grounds exceeded one-third of the escapement into the lake, the sex ratio was in close agreement with the ratio established at the weir.

A predominance of female salmon has occurred each year in the escapement at Bare Lake (fig. 5). This could be due to a higher percentage of females in the annual smolt migrations. The sex ratio of Bare Lake smolts has not been determined, but at Karluk Lake (Barnaby 1944) and Cultus Lake (Foerster 1954b), the sexes were found to be equally represented in the seaward migrations. Nevertheless, a predominance of female sockeye salmon also occurred in the spawning migrations to these lakes, and Foerster concludes that males may suffer a higher mortality at sea. A greater ocean mortality of the males could explain the situation at Bare Lake.

It could also be argued that the predominance of female red salmon at Bare Lake is due to the selectivity of gill nets in the Red River district fishery since gill nets account for two-thirds of the catch, with purse seines taking the balance. The selectivity of gill nets in capturing sockeye salmon of certain size ranges is a well-established fact. With the 5½-inch-stretch mesh nets used in the fishery, according to findings of the

Fisheries Research Institute of Seattle, Wash. (unpublished data), the larger 3-year-old ocean-age males would be more available to the nets than the smaller females of that age. During the years 1952, 1954, 1955, and 1956, however, the catch was calculated to range from less than 1 percent to 15 percent of the escapement (table 2). Such a small catch could have had little influence on the sex ratio during those years, although it may have affected the sex ratio in the other years. Both Barnaby and Foerster considered the selectivity of gill nets, but they did not believe this factor could account for the imbalance in sex ratios that they found in the sockeye.

It is of interest at Bare Lake that the ratio of females to males was greater in the 2-year ocean-age group than in the 3-year ocean-age group (fig. 5). Thus, it would appear females have a tendency to return after less time at sea than males. As 2-year ocean-age fish usually comprise a small part of the run, they would have little influence on the sex ratio of the run. It might be concluded that the high percentage occurrence of 2-year ocean-age females is due to their small size which enables them to escape more readily the 5½-inch gill net mesh. The fact they were predominant even in years of very little fishing would tend to discount this. At Karluk Lake, Barnaby (1944) found males predominant in the

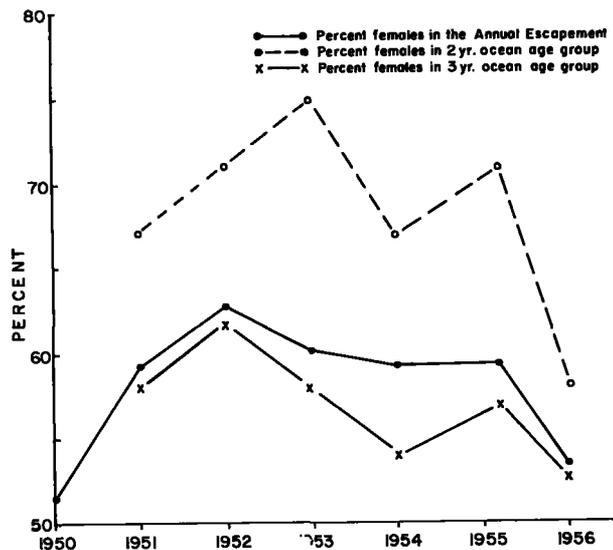


FIGURE 5.—Percentage of female red salmon in the annual escapement and in each ocean-age group.

2-year ocean-age group and females in the 3-year ocean-age group. He mentioned that, since males on the average spend less time in the ocean than females, the mortality of males would be less than that of the females, which should result in a preponderance of males. Actually, the reverse occurs. As he did not think it probable that a differential mortality in favor of the females occurred during the ocean life he had no explanation for this phenomenon. The fact that females predominate in the returns to the three lakes strengthens Foerster's belief that males suffer a higher mortality at sea. For this to apply at Karluk Lake, the greater survival of females would have to exceed the survival advantage male fish might have from a shorter ocean life.

SPAWNING

Once the ocean life of the Bare Lake red salmon has been completed, the fish enter Red River and travel upstream a distance of 16 miles to the outlet of Bare Lake. Upon entering the lake they linger for approximately 2 months before spawning. Duration of this ripening period varies considerably in the different river systems. The period of lake residence averages 1 month in Karluk Lake (unpublished tagging data). In Lakelse Lake, British Columbia, the period averaged 54 days (Fisheries Research Board of Canada, 1954). Howard (1948) found in Cultus Lake, B.C., that the period was approximately 1 month. In the Harrison River system of British Columbia, Schaefer (1951) noted the time was a month or less. It would appear the distance from salt water to a lake has little if any bearing on the length of the red salmon ripening period. Perhaps the length of this ripening interval is a characteristic of particular runs.

To determine the fecundity of Bare Lake salmon, egg counts were made of a few salmon captured at the weir during the years 1952 through 1955. The fork length, weight, age, and egg count by ovary, of the fish sampled is presented in appendix table 1, page 84. It was found that the right ovary of Bare Lake salmon usually contains more eggs than the left ovary. This is rather unusual as the reverse generally occurs with salmon in other areas. It was determined that the fecundity of the fish sampled increased with the age and length of the salmon,

with length accounting for 44 percent of the variation in egg count. As egg counts were not taken in all years, it was necessary to calculate a regression line of egg count on fork length with the existing data. This common regression line was used to estimate the fecundity of the fish each year. It was hypothesized that the regression of egg count on fork length might be the same for all years. Covariance analysis failed to reject this hypothesis at the 5-percent level.

Spawning occurs on certain areas of the littoral zone around the lake; the one tributary stream and several small seepages are not used. During the spawning period, frequent surveys were made of the spawning areas to recover dead fish. All fish recovered were dissected and the sex and spawning condition recorded.

Except in 1950, all eggs retained in the body cavity of partially spawned female salmon were counted. As only two female salmon were recovered in 1951, the sample size was inadequate to determine the average egg retention that year. For the years 1952 through 1956, the mean annual egg retention, which in this calculation included partially spawned as well as unspawned salmon, ranged from 66 to 208 eggs per female (table 5). The mean retention for the 5-year period was 148 eggs per female while the mean retention for partially spawned fish was only 96 eggs per fish. The figure of 148 eggs was used to estimate egg retention in 1951.

Of the female salmon examined on the spawning grounds in 1950, 26.8 percent were totally unspawned. Since no count was made of the eggs retained in the ovaries of spawned fish, the mean egg retention of 96 eggs per spawned female for the years 1952 to 1956 was used. Upon calculating egg retention for all female salmon in 1950, the average retention was found to be 970 eggs per female, or a total egg retention of 28.7 percent of the eggs available for deposition. This loss may have been caused by high water temperatures during the middle of August when the fish were on the spawning grounds. That year the mean surface temperature from August 9 to August 19 averaged 16.9° C., which is higher than the average temperature recorded in the same period during the following 6 years. Foerster (1938) noted a very low egg retention in spawned female sockeye examined on the spawning grounds at Cultus Lake in 1925 and 1935.

TABLE 5.—Annual egg deposition of red salmon in Bare Lake, Alaska

Year	Escapement of females	Mean fork length of females (cm.)	Fecundity ¹	Potential egg deposition	Dead female spawners examined			Corrected egg deposition
					Number	Recovery (percent)	Egg retention per fish	
1950.....	285	57.1	3,374	961,600	71	24.9	² 970	685,100
1951.....	30	57.5	3,417	102,500	2	6.7	³ 148	98,100
1952.....	235	56.6	3,319	780,000	158	67.2	114	753,200
1953.....	146	57.0	3,363	491,000	22	15.1	166	466,800
1954.....	134	54.7	3,112	417,000	64	47.8	208	389,100
1955.....	244	54.5	3,090	754,000	104	42.6	66	737,900
1956.....	185	54.4	3,079	569,600	59	31.9	184	535,600

¹ Fecundity based on regression line of fish fork length on egg count for samples taken during years 1952-55 (9 fish, 1952; 9 fish, 1953; 9 fish, 1954; 16 fish, 1955). Equation for regression line $Y = -2849.18 + 108.98X$.

² Egg retention based on the percentage of unspawned female salmon re-

covered and the mean egg retention of spawned fish for the years 1952-56.

³ Sample size was inadequate, so mean egg retention for years 1952-56 was used.

However, unspawned fish were found dead on the spawning grounds in those years, and if they are included, a mean egg retention of 6.3 and of 19.8 percent occurred.

In table 5, the egg deposition is shown in two ways. The first is based on the escapement, the mean fork length of the females for the year, and the mean number of eggs for that size fish, calculated from the regression formula $Y = -2849.18 + 108.98X$. The second includes a correction applied to those figures based on the mean egg retention of the females recovered on the spawning grounds each year. The largest egg deposition occurred in 1952, yet the escapement that year was smaller than in 1950 and 1955. This indicates that the egg deposition based on the number and fecundity of female salmon in the escapement alone can often be in error. A measure of the egg deposition is important in measuring the survival to later stages in life. Later the survival from egg deposition to the smolt stage will be shown.

EFFECTS OF FERTILIZATION ON YOUNG RED SALMON

FIRST-YEAR GROWTH OF RED SALMON

As previously pointed out, the majority of the adult red salmon spawn during August. By the first part of November the lake is generally covered with ice and remains thus until the following April or May. Seine hauls indicate the young emerge from the gravels during May and June. The time of emergence is dependent upon the time of spawning and water temperatures during the incubation period.

If fertilization is augmenting the food supply of the young red salmon, one of the first indications probably would be the increased growth of

the young fish. To determine if such an increase occurred, seine hauls were taken each growing season during this investigation. The fish captured were counted and a sample of juvenile² red salmon was anesthetized, after which lengths and weights were recorded and scale samples were taken. The salmon were held in live boxes to recover from the anesthetic and were then released into the lake. The catches included young red salmon of three age groups with the fish from the hatch of the year being the most prevalent. Although the three age groups generally can be easily separated by lengths, scales were taken from each fish sampled to validate the age determination.

The growth of red salmon during their first year of life in the lake is shown in figure 6. As noted in the figure, a rather progressive increase in growth occurred during the years 1950 through 1955. It is unfortunate that more seine hauls were not taken in 1950; however, it is believed that the length of the fish taken then is representative of the growth at that time. The rather sharp decline in growth rate during 1956 is discussed in a later section.

AGE COMPOSITION AND SIZE OF SMOLTS

At Bare Lake the majority of the red salmon smolts migrate to sea at the beginning of their second or third year of life. Occasionally, a few fish remain until their fourth year, but only rarely do the fish leave the lake in their first year or remain as long as their fifth.

The smolt migration commences the latter part of May each year, reaches a maximum during

² Stages of the life history of red salmon used in the text are defined as follows: Fry—the period following the absorption of the yolk sac up to the time of active feeding; juvenile—the period commencing with feeding to the time of seaward migration; smolt—the period of migration from fresh to salt water.

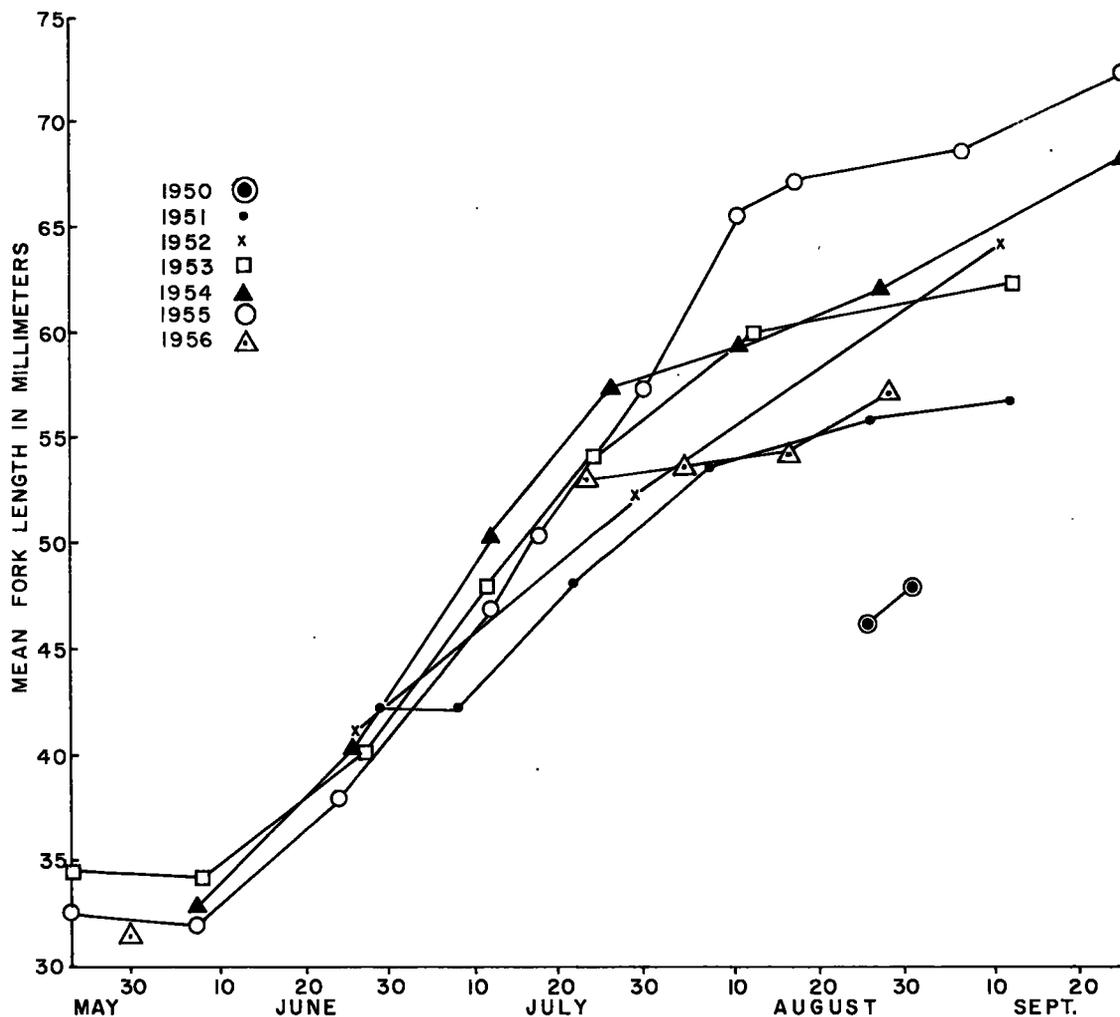


FIGURE 6.—Growth curves of red salmon during their first summer in Bare Lake.

June, and is generally over by the end of July. Unlike in most other areas, smolts in Bare Lake tend to leave the lake during the day on their seaward migration. The reason for this is not known, although large migrations have been witnessed occasionally at Karluk Lake during daylight hours and have also been reported from other areas.

Each day during the migration, the smolts were counted, and a sample was taken to determine the age composition, weight, and length of fish in the migration. The trap (fig. 2) is of simple construction. The smolts migrating downstream tail first are led into the trap. They were captured with a small seine and transferred into tubs of water; the species were sorted and counted; the red salmon smolts were placed in a

live box, and other species were released below the weir. During days of large migrations the trap was seined frequently and the red salmon smolts were accumulated in the live box. At the end of the day a sample of the catch was taken for processing. The live box has two compartments of equal size separated by a removable partition. To obtain a sample of the catch, the partition was lowered to divide the catch in half. One-half was released in the stream below the weir and the remainder subdivided if necessary until a sample of 50 to 100 fish was obtained.

Once the sample of fish was separated from the daily catch, the sample was placed in a tub of fresh water. From the tub a few fish at a time were dipped into a bowl containing a 0.5-percent solution of urethane. After the fish were

anesthetized, fork lengths and scale samples were taken, and each fish was weighed on a beam balance having a sensitivity of 0.01 gram. Before the first fish was weighed, the balance pan was wetted down and the weight of the wet pan set at zero grams. In standardized manner, a fish was placed on the pan, weighed, and transferred to a container of fresh water. Before the next fish was weighed the pan was given a quick shake to eliminate the bulk of the water that had drained from the fish. Periodically the zero setting was checked. By this method, the weight of the fish as recorded here actually includes a film of water that amounts to about 3 percent of the body weight. The smolts were held in the live box for several hours, or until they appeared fully recovered, and then were released to continue their seaward migration. Mortality has been very slight in this operation, and fish were held as long as 2 days without showing signs of distress from the handling and anesthetic.

In appendix table 2, data are presented showing by weekly periods the migration, age composition, mean length, and mean weight of smolts

in each age group during the years, 1950-56. Also given is the number of smolts sampled each week from which the measurements were derived.

The weekly age composition of smolts during the season has followed a rather consistent pattern from year to year. In general, the older smolts migrate to sea earlier in the season. In the years of study the 2- and 3-year-old smolts have accounted for over 99 percent of the annual migrations while the 1-, 4-, and 5-year-old smolts make up the balance. Because the minor age groups make up such a small part of the migration, they are discussed only briefly.

Figure 7 shows the percentage of 2-year-old smolts in the weekly migrations during the years 1950-56. Although the 3-year-old smolts are not shown, it is easy to visualize the complement of the curves presented. Usually the bulk of the 3-year-old smolts has migrated by early June while the 2-year-old smolts migrate in their greatest numbers the latter part of June. In 1950 and 1954, some variations occurred in the normal migration. In the former year, over 60 percent of the July migration was composed of 3-year-

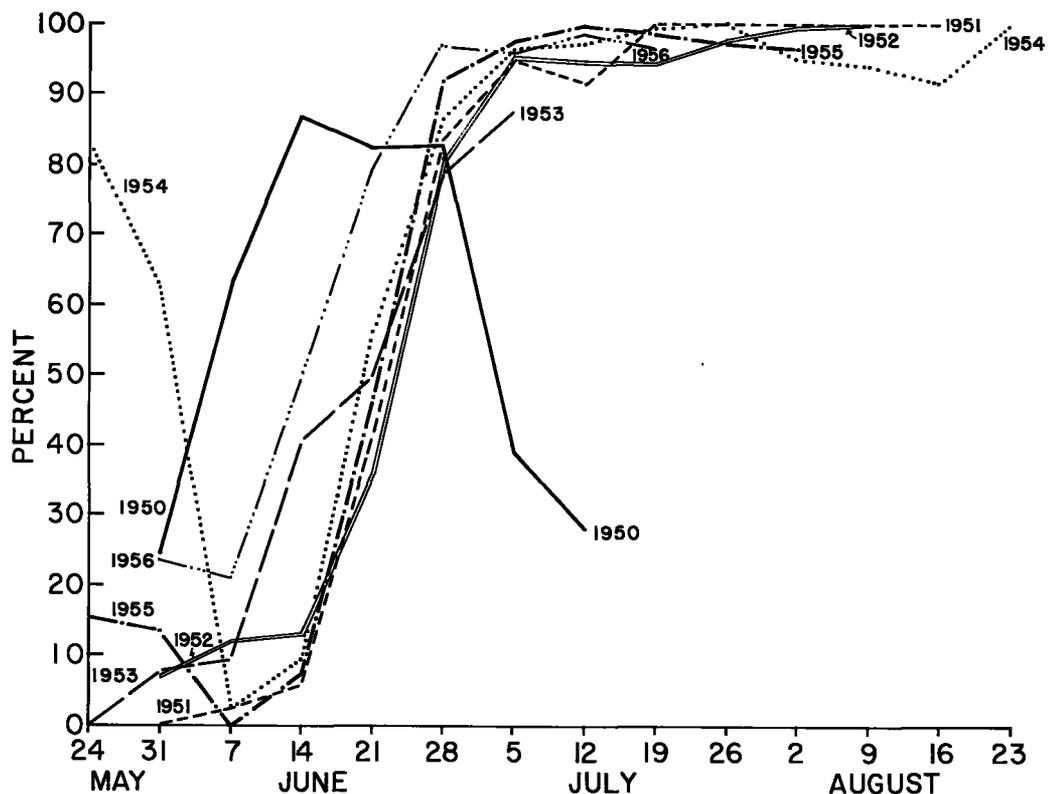


FIGURE 7.—Curves showing the weekly percentage of 2-year-old red salmon in the annual smolt migrations.

old smolts, while during May 1954, 2-year-old smolts predominated over the older fish. Very few fish migrated during these periods; but that does not account for the unusual age composition, for which there does not seem to be a satisfactory explanation.

The percentage of 2-year-old red salmon in the annual smolt migration has ranged from a high of 86 percent in 1954 to a low of 23 percent in 1951 (fig. 8, *c*). A comparison of the annual percentage composition of 2-year-old smolts with the size of the smolt migration (fig. 8, *d*), shows that in years of large smolt migrations (1950, 1954, and 1955) the younger smolts predominated. This no doubt applied also to the smolt migrations of 1947 and 1949. From each of these migrations large numbers and a high percentage of the 2-year-old smolts returned 3 years later as adults at age 5₂ (table 4). For this to occur, the smolt migrations in those years must have been large and made up mostly of 2-year-old fish.

To determine the effect that the number of smolts produced by a brood year might have on the age at which they migrate to sea, a calculation was made of the number of smolts produced by brood years 1948-53 and the percentage of smolts which migrated to sea from each brood as 2-year-old fish. It was found that approximately 60 percent of the variability in the percentage of smolts migrating to sea in their second year was associated with the number of smolts produced in a brood year. Greater percentages of smolts migrated to sea at an earlier age from brood years of high production than from years of low production. Possibly population pressure caused the bulk of fish in the big-brood years to migrate earlier. This could account for the low populations of 3-year-old smolts, because only in brood years of low smolt production could they dominate in numbers over the 2-year-old smolts. Also, limiting the abundance of the older smolts would be the additional mortality imposed on this group by the extra year in fresh water.

There is a general tendency for the slower-growing fish in the population to migrate later in the season or remain in the lake another year. This is apparent over the years and is shown in a comparison of the length curves each season of 2-year-old smolts taken in the smolt trap and 2-year-old juvenile red salmon captured in seine

hauls (fig. 9). However, size alone appears to have little influence on the age composition of the smolt migration. The increase in size of smolts since 1950 has not brought about an increase in the percentage of younger smolts in the annual migrations.

A considerable increase in the size of smolts has occurred since 1950. The smolts of 1950 could receive no benefit from the first fertilization of Bare Lake, as they migrated before the application. The rather progressive increase in length and weight of smolts, which occurred, built up to a peak in 1955 and declined somewhat in 1956 (fig. 8, *a* and *b*). The smolts of 1955 in all age groups were more than 30 percent longer and more than 150 percent heavier than those of 1950. During the years 1951-55, increase in size of smolts was rather consistent among all age groups. Upon comparing figures 8, *a* and 8, *b* with figure 8, *d*, no relation is found between the size of the migration and the increase in length or weight of the smolts during the years of study. More often, as reported by others, there is a tendency for smolts to be small in years of large migrations. Evidently this did not take place at Bare Lake as the food supply of juvenile red salmon was adequate even in years when they were abundant.

Information was obtained on the size of smolts in the years 1947, 1948, and 1949 through use of a procedure involving scale radius measurements. The method involved taking scale-radius measurements from 100 smolts each of 2- and 3-year-old fish for the years 1950 through 1953. It was determined that a highly significant correlation ($r = .983$; $P < .01$) exists between scale radius and fork length of smolts when the age groups are kept separate. When the age groups were combined for each year, the correlation between mean annual length and mean scale radius weighted by the age composition of the migrations was found to be significant at the 5-percent level in which $r = 0.91$.

Since a relation existed between the scale radius and size of the smolts, it was necessary to show agreement between the fresh-water scale radii of the adults and the scale radii of the smolts that produced the adults. To do this, scale-radius measurements of the fresh-water growth were taken from almost all of the adult

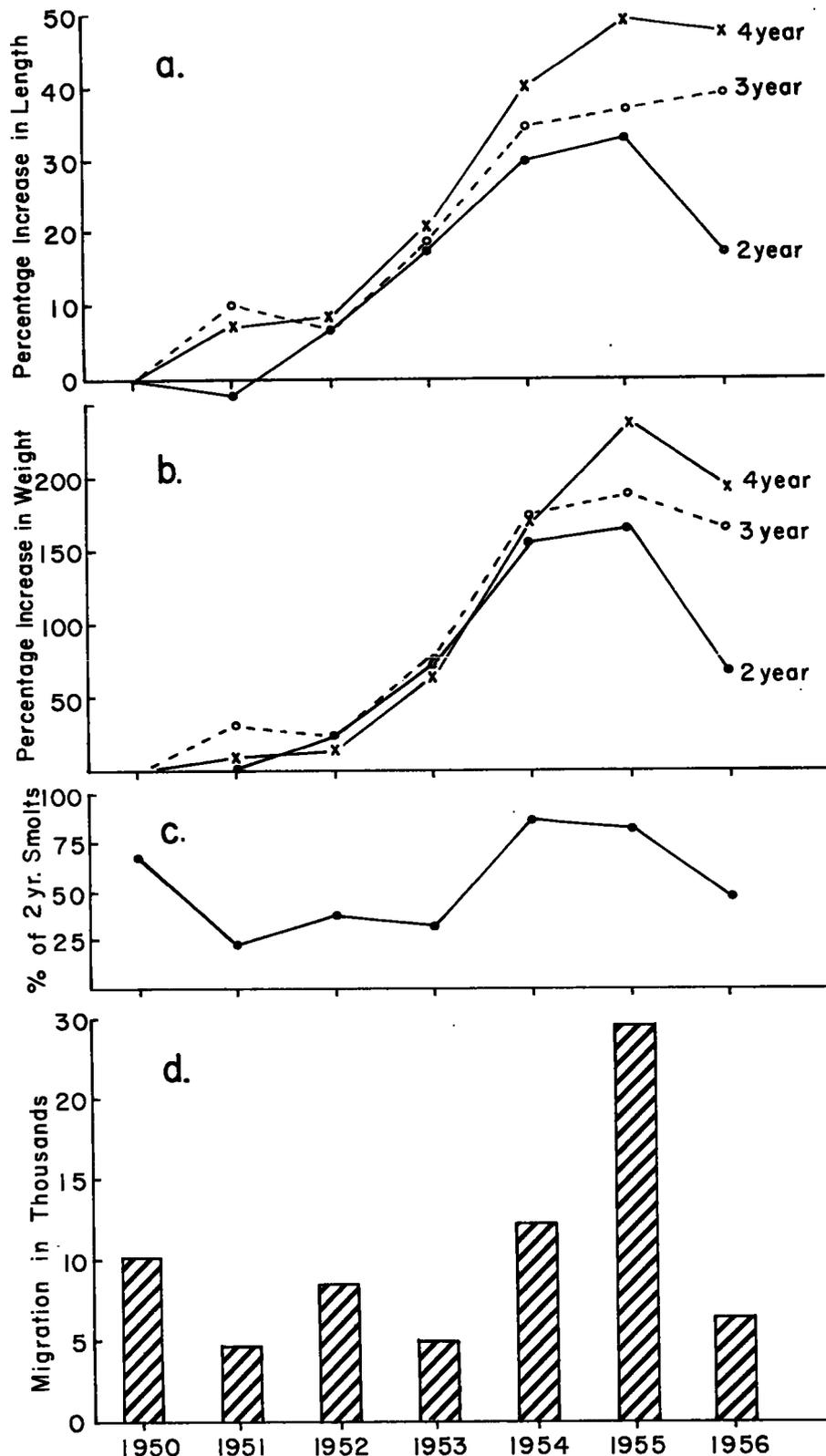


FIGURE 8.—Relation between size of the smolt migration and (1) the age composition and (2) increment in smolt length and weight. a. Percentage increase in length of smolts between 1950 and the years 1951 to 1956. b. Percentage increase in weight of smolts between 1950 and the years 1951 to 1956. c. Percent of 2-year-old smolts in the annual migration, 1950 to 1956. d. Total annual smolt migration, 1950 to 1956.

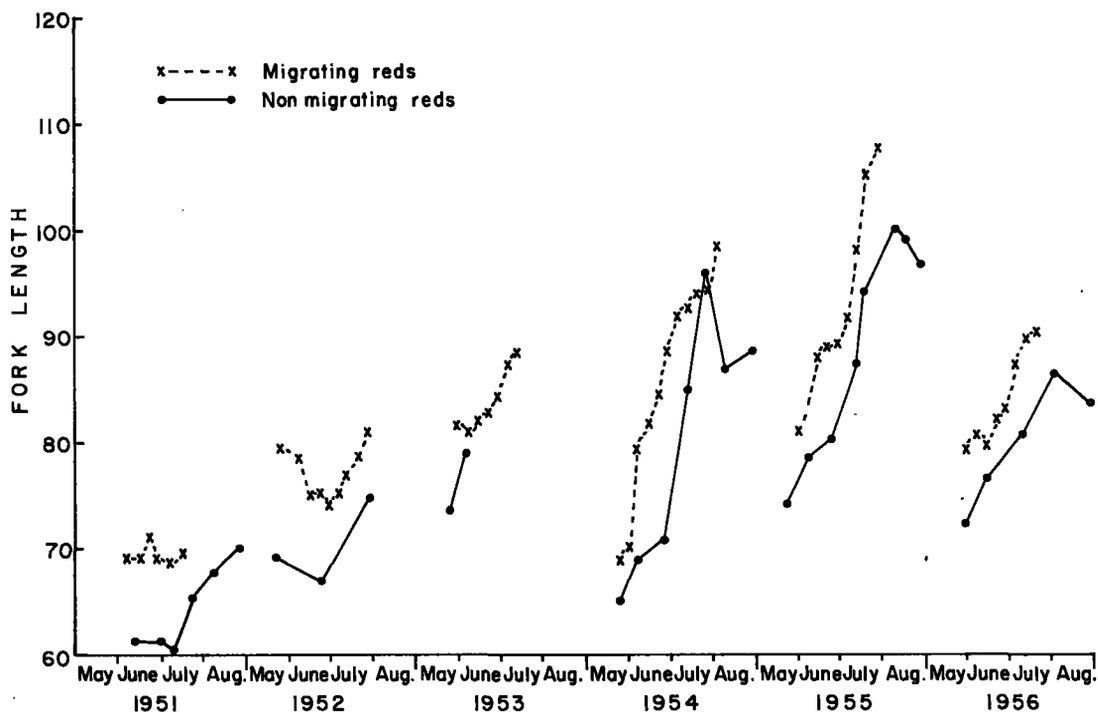


FIGURE 9.—Fork length (in millimeters) of 2-year-old migrating and of 2-year-old nonmigrating red salmon juveniles, Bare Lake, Alaska, 1951-56.

salmon in the escapement produced by the smolt migrations of 1950 through 1953. In several instances, returns of adult salmon by individual fresh-water age were quite small, so the age groups were combined. The mean scale radius and length of smolts for the years 1950 through 1953 and the mean fresh-water scale radius of adults returning from each of these migrations are shown in table 6. Comparative data for the 4 years show the fresh-water-zone scale radii of returning adults were larger than or equal to those of the smolts producing them. The increase probably is caused by a greater mortality of the smaller smolts at sea. Measurements of the fresh-water-zone scale radius were also taken from scales of adult salmon returning from the smolt migrations of 1947 through 1949, and data in table 6 indicate that these radius measurements were slightly smaller than those of the adult salmon in 1950. This is good evidence that the smolts of 1947 to 1949 were smaller than those of 1950, although it does not necessarily mean they were smaller in all age groups.

TABLE 6.—Weighted mean length and mean scale radius of 2-year-old and 3-year-old smolts combined and mean fresh-water-zone scale radius of adults returning from the smolt migration

Year of smolt migration	Combined 2- and 3-year-old smolts		Mean fresh-water scale radius of returning adults (mm.) ¹
	Mean length (cm.)	Mean scale radius (mm.)	
1947.....	0.29
1948.....28
1949.....30
1950.....	72.8	0.28	.32
1951.....	81.8	.34	.37
1952.....	79.1	.32	.32
1953.....	90.2	.39	.41

¹ Combined 2- and 3-year-old fresh-water age groups.

RELATION BETWEEN RED SALMON GROWTH AND RATE OF PHOTOSYNTHESIS

As pointed out previously, the size of the red salmon increased progressively between 1950 and 1955. A decline in size occurred in 1956 among the fry and 2- and 4-year-old smolts. Although the 3-year-old smolts in 1956 were slightly larger than those of the year before they weighed less (fig. 8, b) which indicates poor growing conditions. Curves showing the trend in size of fish

in each group for years 1950-56 are presented in figure 10, *a*. Juvenile lengths are based on the length the fish attained on August 27 of each year, as shown in figure 6. That date was selected since it is the latest date in the season for which length data were available for all years. Annual mean smolt length of each age group was determined by sampling throughout the period of smolt migration.

The observed progressive increase in fish size might be expected, because the organisms the fish eat are relatively long lived, and some time would be required for the population to build up in response to an increase in food supply brought about by fertilization. The decline in 1956 was unexpected, and an effort was made to determine the cause. Possible explanations for this decline, particularly temperature and primary food production, were examined. Air temperatures taken at Kodiak, 80 miles northeast of Bare Lake, were examined for the months from September 1955 to May 1956 and for like periods in the preceding years. Temperature data were insufficient from Bare Lake; however, for the months in which temperatures were recorded, they were closely correlated with temperatures at Kodiak.

The mean temperature at Bare Lake from September 1955 to May 1956 was 33.7° F., which was 2.5° below the mean for like periods of the preceding 6 years. Furthermore, each monthly mean temperature was lower than the monthly mean temperature of the 6 previous years. The air temperature could hardly influence the water temperature once the lake was frozen, but a prolonged period of low air temperatures could increase considerably the thickness and duration of the ice cover. Also, because of the severity of the conditions at time of freezing, the lake water may have been at a somewhat lower

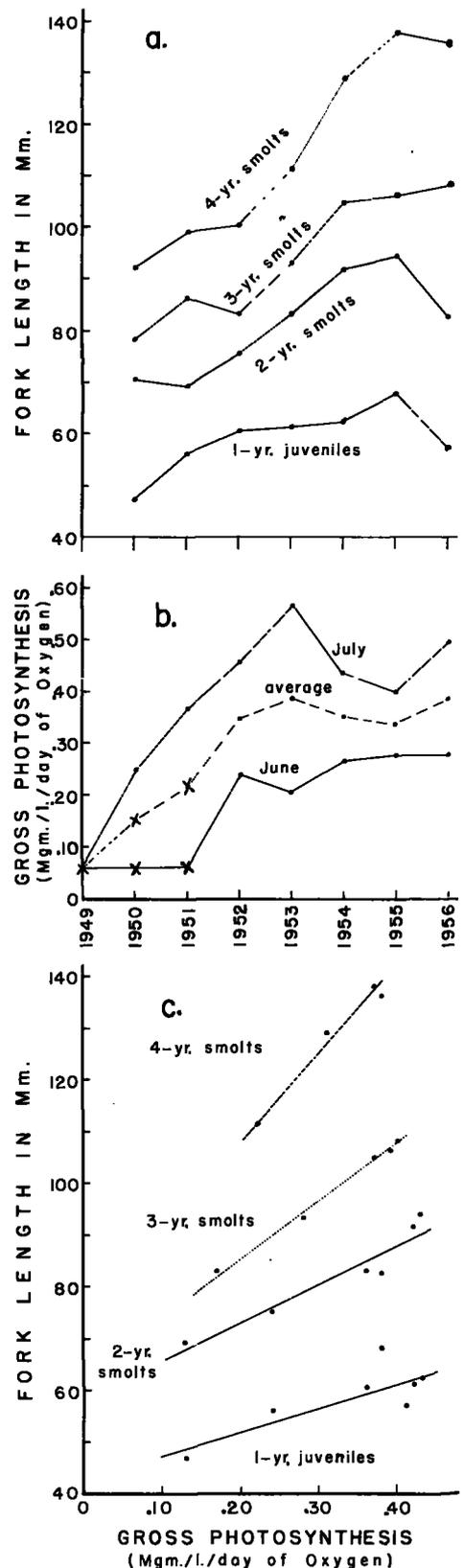


FIGURE 10.—The relation between gross rate of photosynthesis and growth of red salmon juveniles. *a*. Curves showing the mean length of juvenile red salmon on August 27 of their first growing season and of red salmon smolts migrating to sea in the beginning of their 2d, 3d, and 4th year of life for the years 1950-56. *b*. Curves showing the mean rate of gross photosynthesis during the years 1949-56 for the 40-day periods after the June application of fertilizer and for a similar period after the July application. Also presented is a curve of the average of the two periods for those years. Points on the curves marked by an x denote that the values are estimated or partly estimated. *c*. Scatter diagrams showing the relation between gross photosynthesis and fork length for each age group of fish. Regression lines are drawn by inspection.

temperature than at the time of freezing in other years. These conditions could have resulted in reduced growth and increased mortality of fish food organisms and may have had some effect on the fish themselves. When all years were considered, however, no relation was found between mean temperatures during this period or during the summer period and fish growth.

The data gathered each year on growth rate of young salmon and primary productivity as measured by the rate of photosynthesis of the phytoplankton were examined to determine if a relation existed between them. If a relation was found it would tend to substantiate the proposition that the salmon population is held in check by insufficient food and would provide an explanation for the decline in fish growth during 1956.

Plotted in figure 10, *b* are the mean rates of gross photosynthesis, determined by the method described by Nelson and Edmondson (1955), for the 40-day period after each June and July application of fertilizer and the average rate of the combined periods. The gross rate of photosynthesis for the period after the July fertilization increased progressively each year up to 1953, was considerably lower in 1954 and 1955, and increased again in 1956. The rates of photosynthesis after the June fertilization show a different trend during the years 1952-56. Unlike in the later period, a small decline in rate of photosynthesis from 1952 occurred in June 1953, and a progressive minor increase occurred in subsequent years. As photosynthetic activity was greatest after the July fertilization, the curve of the combined periods followed a similar pattern although the fluctuations were smaller. No actual measurements were made in 1949 when the lake was not fertilized, but on the basis of measurements made just before fertilizing the lake in July of 1950 and 1951 (Nelson and Edmondson, 1955), it is believed the mean rate of oxygen production would not have exceeded 0.12 mgm. per liter per day and may well have been about 0.06. This figure is plotted as the rate during 1949 and during the early part of the 1950 and 1951 seasons when the lake was not fertilized in June. The causes of the fluctuation in rates of photosynthesis during these years has not yet been analyzed, but the changes are of considerable magnitude, particularly in July.

A cursory comparison of the curves of seasonal rate of photosynthesis with the size of young red salmon reveals a certain correspondence between them (fig. 10, *a* and *b*). To show the relation more clearly, correlation diagrams were made (fig. 10, *c*). In the case of juvenile red salmon in their first growing season, it was thought three periods in time would be important in affecting the population size and growth of the new crop of insect larvae hatching in early summer and which would be fed upon by salmon hatching that spring. The period after the July fertilization of the previous year was considered important to the survival of the brood stock of insect larvae that was to produce the new generation utilized by the recently hatched fry. Periods after both the June and July fertilizations would influence the growth and survival of the newly hatched larvae. Thus, in figure 10, *c* for the years 1950-56, the length the juveniles attained on August 27 of their first growing season is plotted against the mean rate of photosynthesis after June and July fertilizations of that year and after July fertilization of the preceding year. All three periods were weighted equally in establishing the mean.

To show the relation between smolt size and rate of photosynthesis, the mean fork length of smolts for each age group was plotted against the mean rate of photosynthesis over those periods mostly responsible for the development of insect larvae upon which the fish fed during their lake residence. As the bulk of the smolts usually migrated prior to the third week in June during the years of study, the period after the June 10 fertilization in the year of smolt migration would be of little or no value in providing fish food organisms for the smolts before they migrated. However, conditions in the preceding years would affect the food supply of these fish, with the older smolts being subjected to the environment for the longer period of time.

The following example shows the procedure adopted in making the scatter diagrams (fig. 10, *c*) for smolts of various ages: The mean fork length of the 2-year old smolts migrating to sea in 1955 was plotted against the mean rate of photosynthesis in the fall of 1953 and during 1954; the mean fork length of the 3-year-old smolts migrating the same year was plotted

against the mean rate of photosynthesis during the years 1954 and 1953 and the fall of 1952; correspondingly, the mean fork length of 4-year-old smolts in 1955 was plotted against the mean rate of photosynthesis for the years 1954, 1953, 1952, and the fall of 1951. The rate of photosynthesis over each 40-day period was given equal weight in establishing the mean rate.

A good relation between fork length and rate of photosynthesis was found in smolts (fig. 10, c). The relation was weaker in fry. Perhaps sampling in the lake was inadequate to establish with sufficient accuracy the size of the juveniles on August 27. Nevertheless, the decline in rate of photosynthesis during 1954 and 1955 appears to have had considerable effect on the size the fish achieved in 1956. The relation between fork length and photosynthetic rate indicates a much closer dependence of fish growth on primary photosynthetic productivity than might have been expected *a priori*.

Phytoplankton is immediately or indirectly available to zooplankton and to many of the bottom organisms which are used as food by the salmon. Since so many steps exist between the original synthesis of food materials by the phytoplankton and the growth of the salmon and since fish are affected by so many environmental factors in addition to food supply, one might not expect a relation to exist between salmon growth and photosynthetic rates of the phytoplankton. Since such a relation does exist, it might be understandable in terms of the food chain involved. A higher primary production would result in a better state of nutrition of the crustaceans, insect larvae, and other animals on which the fish feed. The food animals would grow larger and be more nutritious to the fish. Adult insects produced from well-fed larvae would presumably be able to lay more eggs, and this would increase the potential population of insect larvae in the lake.

It will be interesting to follow this relationship when fertilization of Bare Lake is discontinued. Furthermore, it will eventually be possible to make a rather complete assessment of food conditions at Bare Lake when all the time-consuming censuses of plankton and bottom fauna are finished.

EFFECTS OF FERTILIZATION ON RED SALMON SURVIVAL

FRESH-WATER SURVIVAL

It is hypothesized that fertilization of Bare Lake increases the fresh-water survival of young red salmon. To determine this requires many years of observations. For example, to measure survival from one brood year to the smolt stage requires an enumeration of the number of smolts of that brood migrating seaward 2, 3, 4, and 5 years later. Up to the present time no measurements have been made of the fry hatch from known egg depositions. In fact, very little has been done in other areas toward measuring fry production from a beach spawning area because of the many difficulties involved in conducting such work. If this could be done it would be extremely useful in evaluating the effect of meteorological conditions on the eggs over winter. To some extent, conditions that produce poor survival to the smolt stage might in part be created during the period the eggs are in the gravels rather than during the free-swimming period in the lake. In such a case any benefits fertilization might have on survival would be masked.

Survival to the fry stage has been measured in several streams in British Columbia. In Scully Creek, a small tributary of Lakelse Lake, fry production for 5 years averaged 11.8 percent (range, 9.3 to 13.7); Williams Creek, located in the same system, had a production of approximately 7.5 percent in 1954; Six Mile Creek, Babine Lake, had survivals of 19 percent in 1954 and 12 percent in 1951; Port John survivals were 13.4 percent in 1954, a mean of 9.5 percent for earlier years, with a range of approximately 1.7 to 25.5 percent (Fisheries Research Board of Canada, 1955, p. 81). The range of fry production at Scully Creek was small over the 5-year period, but at Port John the range was large.

Because of lack of information on survival to the fry stage at Bare Lake, the range in fry survival is not known. To determine if fertilization has increased survival of red salmon from the egg to the smolt stage, will require that observations be made both during the years of fertilization and those of no fertilization.

At the present time rates of fresh-water survival have been measured from the brood years of

1950 through 1953. During those years an increased survival was indicated which could have been caused by a buildup of nutritional benefits. As shown in table 7, the average annual survival rate during the period was 2.96 percent. These survivals are based on egg depositions (table 5), with the correction applied to unspawned and partially spawned fish. In many areas, this correction has not been so readily assessed; hence, survival rates have been based on the potential egg deposition, as determined from the number and fecundity of female salmon in the escapement. When no correction is made to Bare Lake data, the mean survival rates during the years average 2.76 percent (range, 0.74 to 4.86)—a survival somewhat greater than has been reported from other areas. Barnaby (1944) found the fresh-water survival of Karluk River red salmon usually to be less than 1 percent. He suggested that the survival is low because the fish have a longer residence in fresh water. Measurements of fresh-water survival at Cultus Lake, British Columbia, during 1925, 1927, and 1930 were 1.13 percent, 1.05 percent, and 3.16 percent, respectively (Foerster 1936a). The smolts ranged in length from 2 to 4 inches, which would be comparable in size to the smolts of Bare Lake. At Lakelse Lake, Brett and McConnell (1950) report survivals of 1.1 percent, 0.4 percent, and 1 to 2 percent during the years 1946 through 1948. At Babine Lake, British Columbia, survivals of 0.48 percent, 0.77 percent, 1.57 percent, and approximately 2 percent were found for the years 1949 through 1952, respectively (Fisheries Research Board of Canada, 1955). From Dombroski (1954), the average lengths of Babine Lake smolts for years 1950 through 1953 were 83.1 mm., 82.5 mm., 80.6 mm., and 86.5 mm., respectively. During this period these fish averaged slightly longer than Bare Lake smolts. The lower fresh-water survival of Babine Lake red salmon may be compensated by the larger size of smolts migrating to sea.

The fresh-water survival values of red salmon at Bare Lake were measured during the years the lake was fertilized. Although the fresh-water survival at Bare Lake averages slightly higher than reported from other areas, this could be normal. With a high average fresh-water survival, the marine survival might be expected to be lower than the normal; otherwise, produc-

TABLE 7.—*Fresh-water survival of young red salmon in Bare Lake, Alaska*

Brood year	Egg deposition	Downstream smolt production ¹				Survival (percent)
		2 years	3 years	4-5 years	Total	
1950	685, 100	3, 668	3, 441	51	7, 160	1.05
1951	98, 100	1, 644	1, 692	292	3, 628	3.70
1952	753, 200	10, 532	4, 311	46	14, 889	1.98
1953	466, 800	20, 033	3, 308	50	23, 841	5.11

¹ Including mortalities at the trap.

² Estimated.

tion would be unusually high compared with other areas. It is possible that a compensating factor operates, so that if fresh-water survival is low marine survival is high, and vice versa.

For fertilization to increase survival, it should indirectly create more food for the young red salmon. With an increase in food, growth would be increased before survival would be improved, as is indicated in the preceding section. To determine the end product in the food chain from fertilization of the lake to food of the young red salmon, the stomach contents of 150 juvenile red salmon were examined, including 51 smolts, 10 juveniles taken during February 1955, and 89 juveniles taken in seine hauls during the following summer. The diet of the young fish, including the smolts, taken during May through September, consisted mostly of bottom fauna with chironomids comprising the major part. The fish taken during February 1955 from under the ice were found to be feeding chiefly on ostracods and copepods.

OCEAN SURVIVAL

Measurements of the fresh-water survival, as described in the preceding section, represent only a portion of the life of the red salmon. Once the smolts leave the lake for their ocean sojourn, they are subjected to a new set of environmental hazards that may be very important in determining the survival rate. For comparison with results at Bare Lake, other observations on ocean survival of red salmon will be briefly reviewed.

The most comprehensive studies of ocean survival of red salmon have been made by Foerster (1934, 1936b, 1954a) at Cultus Lake and by Barnaby (1944) at Karluk Lake. In the former investigations, all smolts were captured at the weir and the annual seaward migration was enumerated. During each of the 3 years following

each smolt migration, the age composition of the escapement was determined, and from this the number of adults in the escapement returning from the smolt migration was calculated. As the Cultus run makes up a small portion of the Fraser River run, and, since the catch usually exceeds the escapement, it was difficult to assess the portion of the fish returning to Cultus Lake that were taken in the fishery. To measure the total return of smolts as adults, during 1930 and 1931 all the smolts were marked by clipping a different combination of fins each year. Thereafter, fish returning to the weir and taken in the fishery as adults were examined for marks. The percentage of marked fish returning from each year's marking indicated the ocean survival. Foerster (1936b) reported recoveries of 3.67 percent and 3.5 percent from the two markings. Previous marking experiments, however, had indicated that marked fish suffer a 62-percent differential mortality over unmarked fish. Upon correcting for this loss, he concluded that the most probable survival during those years was approximately 9.9 percent. For other years at Cultus Lake, Foerster (1954a) presents a table of the smolt migrations and the percentage survival of smolts that returned in the spawning escapement only. The survival rates ranged from 0.31 to 6.68 percent, with a mean of 2.74. From recoveries of marked fish in 1930 and 1931 the catch accounted for one-half of the recoveries in the one year and three-fourths of the recoveries in the other year. If the catch usually takes from one-half to three-quarters of the run, the percentage survival as given by Foerster should be two to four times greater than indicated, if they are to account for the total return of smolts.

During the period in which ocean survival of salmon was measured at Cultus Lake, the smolts averaged 88.2 millimeters in length (range, 66 to 107) and 7.47 grams in weight (range, 2.7 to 12.8). In regard to the relation between ocean survival and smolt size Foerster (1954a) concluded—

Analysis of these data indicated a negative correlation between size of migration (in number of smolts) and percentage return of adults which is found (by multiple correlation treatment) to be related principally to the size (weight in grams) of the smolts.

In a somewhat different manner, Barnaby measured the ocean survival of Karluk smolts. Re-

sults of his studies showed a greater survival in the ocean among the older and larger 4-year-old smolts than among the smaller 3-year old smolts. Average survivals for 6 years for the two groups were 25.7 percent and 17.4 percent, respectively. Average survival for all age groups was 21.4 percent. Barnaby points out that these high survivals were due to the large size of the smolts. As shown in the table of smolt sizes which he presents, the fish averaged approximately 137 millimeters in length and 24 grams in weight during the years of study.

By using table 4, the number of smolts returning as adults from the Bare Lake smolt migrations of 1950 through 1953 can be determined. For example, from the 1950 smolt migration, 3 adults returned as age-group 4₁ in 1953, 13 adults as 4₂ in 1952, 271 adults as 5₂ in 1953, 30 adults as 5₃ in 1952, and 16 adults as 6₃ in 1953. Summing these returns gives a total of 333 adults returning from the 1950 smolt migration. The number of fish returning and percentage return from this migration and subsequent smolt migrations is shown in table 8. This table, patterned after Foerster's table (1954a, p. 342), shows the relation between the size and number of smolts and the return of smolts as adults. The percentage of smolts returning (ocean survival) increased during the 4 years. This corresponds with an increase in size of smolts during the period and is in agreement with the work of Barnaby and Foerster previously mentioned. The slight discrepancy in the relation between size and percentage return in 1951 and 1952 probably is not significant, since size of the smolts and percentage return are quite similar.

It is of interest that the return of adults from the smolt migration of 1953 was greater than from that of 1950 although the migration of 1953 was less than one-half as large as that of 1950. This resulted from the increased survival at sea of the large smolts migrating in 1953. Possibly these smolts, by being larger and more vigorous, were better equipped to evade predators and withstand other hazards of their early life at sea. Thus, fertilization in an indirect manner may have caused a profound effect on survival. On the basis of the large smolt migrations of 1954 and 1955 and the large size of the smolts since 1953 (table 8), we might expect good returns of adult

salmon during the years 1957 and 1958.³ Adverse ocean conditions could influence the number returning and in fact, this factor probably accounts in part for the wide range in returns found by Foerster at Cultus Lake.

TABLE 8.—Annual smolt migration, mean annual lengths and weights of smolts, and number and percentage of smolts returning as adult salmon, 1950 through 1956

[All age groups combined]

Year	Smolt migration			Returning adults	
	Number	Mean fork length (mm.)	Mean weight (gm.)	Number	Percentage of smolt migration
1950.....	10,199	73.2	3.35	333	3.26
1951.....	4,503	82.2	4.83	205	4.55
1952.....	8,020	80.5	4.59	457	5.30
1953.....	5,058	90.2	6.54	399	7.89
1954.....	12,189	93.7	8.23
1955.....	24,100	97.2	8.99
1956.....	6,525	97.0	8.23

EFFECTS OF FERTILIZATION ON OTHER FISHES

In addition to red salmon, Bare Lake supports populations of six other fish species, coho salmon (*Oncorhynchus kisutch*), king salmon (*Oncorhynchus tshawytscha*), steelhead trout (*Salmo gairdneri*), Dolly Varden charr (*Salvelinus malma*), sculpin (*Cottus aleuticus*), and the three-spine stickleback (*Gasterosteus aculeatus*). Of these species, juvenile king salmon, steelhead trout, and sculpin are present in small numbers and probably have little effect on the general ecology of the lake. The other species are important as predators or competitors of juvenile red salmon. Of interest in this study is the effect fertilization of the lake may have had on these species.

Only limited observations were made on fish populations other than red salmon in Bare Lake during the years 1950 to 1954.

Observations on the growth and population size of Dolly Varden charr were initiated in 1954 and expanded in 1955. These are to be

³ Data that have become available since completion of this report show that in 1957 approximately 265 red salmon returned. From stream surveys of Bare Creek. It is estimated that the stream was impassable to salmon from the period July 1 to July 19. Lack of rainfall created this condition. The blocking of the migration during this period might at least in part explain the poor run. The run in 1958 was the largest on record. Although no weir was maintained in Bare Creek this year, 914 red salmon were recovered on the spawning grounds. Upon considering the number of salmon not recovered on the spawning grounds and the number taken in the fishery, it is estimated that the 1958 run was approximately 2,000 red salmon.

reported by C. S. Thompson at a later date. In addition, some samples of coho smolts have been obtained since 1954 for determination of age and size composition. At the smolt trap, records have been kept of the number of coho and red salmon smolts, Dolly Varden charrs, and steelhead trout migrating to sea (table 9). Included in the coho count are a few king salmon smolts, which closely resemble coho smolts; time did not permit the necessary careful examination for separate counts.

TABLE 9.—Number of coho smolts, Dolly Varden charr, and steelhead smolts in seaward migration, Bare Lake, Alaska

Year	Coho ¹	Dolly Varden charr	Steelhead
1950.....	1,134
1951.....	2,389	2,733	21
1952.....	1,781	3,905	48
1953.....	2,014	797	13
1954.....	3,341	1,058	23
1955.....	3,247	2,390	31
1956.....	2,946	2,777	26

¹ May include some king salmon smolts.

Coho salmon.—As shown in table 9, there is some indication of an increase in the coho population over the years. As adult coho salmon do not enter Bare Lake until after the weir is removed, we have no measure of the size of the spawning population. Thus, an increase in numbers of smolts may be caused by an increase in egg depositions rather than by an increase in survival. Because we do not have adequate data on spawning populations, it is not possible to determine the fresh-water survival rates. Also, length data of coho smolts is insufficient to determine if fertilization might have brought about an increase in the growth rate during the years of study.

The coho smolts migrate to sea in their second or third year and are, in general, larger and more robust than the red salmon smolts. The stomach contents of a few cohos have been examined. During the summer, juvenile cohos feed mostly on insects or insect larvae. To some extent the larger juvenile cohos are predaceous on the juvenile red salmon but, in general, their role seems to be that of competitors for food rather than predators.

Dolly Varden charr.—A fairly large Dolly Varden charr population is present in Bare Lake. This is indicated by the numbers captured in the smolt trap (table 9). It is not known if these counts are indicative of the population which

would have migrated to sea had the trap not been installed. Large charrs cause heavy losses of salmon smolts when the two are confined together. To reduce predation, the opening of the trap was made small enough that large fish could not enter. Occasionally large charrs enter the trap during high water, and some have been captured above the trap and released downstream. To some extent their normal migration has been impeded, so the counts in the table may not be representative of the population normally migrating at this time. To facilitate upstream movement of juvenile coho salmon and Dolly Varden charrs, seine hauls periodically are taken below the trap, and the catch is released in the lake. The marking of these fish has indicated that they are migrating to the lake, as less than 10 percent of those marked have worked back downstream to the weir.

As data are not available on the size of the spawning stock or survival to various stages in the life history of Dolly Varden, it is not possible to say whether fertilization increased survival. Also, samples were inadequate to determine rate of growth during years 1950-56.

Stomach contents of charrs examined during the summer show they feed on caddisfly larvae, winged insects, gastropods, salmonids, and sticklebacks. To a small extent competition for food exists between the small charrs and juvenile red salmon. During the smolt migration, charrs feed to some extent on the smolts; however, their predation on red salmon from May to September does not seem to be important.

Threespine stickleback.—There is a large population of sticklebacks in Bare Lake. Beach-seine catches each year at the north and south ends of the lake show this species to predominate in numbers over juvenile red salmon (appendix table 3). Sticklebacks feed on about the same items of food as the juvenile red salmon; thus, they are direct competitors of the salmon for food. Their abundance is perhaps kept in check because Dolly Varden charrs and cohos feed on them to some extent, which may result in less predation by these species on juvenile red salmon. From seine-haul catches it would seem the peak in abundance of sticklebacks occurred during 1953 and of juvenile red salmon during 1954. Although seine-haul catches probably provide

only a rough index of population size, the fact that the red salmon smolt migration of 1955 was the largest observed during these studies strengthens the finding of juvenile red salmon being unusually abundant during the preceding year.

Growth studies of threespine sticklebacks have been conducted in Bare Lake since 1950. Greenbank and Nelson (1959) present growth curves of sticklebacks for year classes 1951 through 1954. An examination of these data indicate no progressive increase in growth rate occurred. Thus, unlike red salmon juveniles, sticklebacks did not respond to fertilization by increased growth.

DISCUSSION

To understand the effect on the growth of fish of fertilizing a lake with inorganic material, it is necessary to consider the food chain involved. It has been shown that fertilization increased primary productivity in Bare Lake manyfold (Nelson and Edmondson, 1955), and that a large crop of phytoplankton resulted and was maintained during the rest of the summer. This increased food supply would be expected to benefit directly many of the invertebrates. Invertebrates that would be of most direct value to the red salmon are a variety of benthic insect larvae and the planktonic copepod *Epischura nevadensis*. All of these animals have a long life cycle and even the copepod appears to produce but one generation a year. Therefore, an increased food supply would not express itself immediately in an increased number of animals, and the invertebrate populations might well take some years to build up, especially if there is much predation. In fact, during the period 1950-52 the zooplankton population showed no progressive increase. It would seem that a population of active predators with versatile hunting behavior may keep the prey population at a low level and absorb extra production, so that a distinct increase in production may not show up as an increase in the standing crop of food organisms, but rather as an increase in the mass of the predator population.

There are certain immediate effects that might result in better growth of the fish. It has been shown that increases of the food supply for a natural population of the copepod *Calanus fin-*

marchicus were followed shortly by increases in length, weight, and fat content of the mature animals (Marshall, Nicholls, and Orr, 1934). This effect is to be expected with most animals, and it may well be that the food organisms in Bare Lake have provided much more nourishment for the fish since 1950 than is suggested by their numbers alone.

In reviewing the results of fertilization of Bare Lake to date, the most important development is that smolt size has increased. This progressive increase may have brought about the observed increase in return of adult salmon, since larger smolts have been found to survive in greater numbers at sea (Barnaby 1944, Foerster 1954a). Data from 4 years' observations indicate that ocean survival has increased more than twofold. If growth and fresh-water survival rates decline when fertilization is discontinued, the theory that observed increases have resulted from fertilization will be greatly strengthened.

Other factors were examined which might have brought about the increase in length of Bare Lake smolts during 1950 to 1956. At nearby Karluk Lake, the smolt migration was sampled annually for length and age composition. No increase in size of smolts occurred in this unfertilized lake over the 7 years of our Bare Lake study. As stated earlier, no relation could be found between water temperatures and smolt growth at Bare Lake. Diseased juvenile red salmon were uncommon in Bare Lake, which indicated disease was not a factor influencing growth or survival. It might be argued that a decline in population density or intraspecific competition could have brought about the increased growth of red salmon juveniles and smolts during the years 1950 to 1956. This was examined on the basis of population biomass of all species of fish in the lake during those years. From text tables 8 and 9 and appendix table 3, estimates of the biomass of fish present in the lake were made from both seine-haul and weir-count data. No relation could be found between the biomass of all fish or the abundance of certain fish species and the size attained by the young red salmon. On the contrary, it appears a slight increase in biomass of fish occurred while at the same time the size of red salmon smolts and juveniles increased. Evidently the increment in fish food brought about by enrichment of the lake was of such magnitude

that the influence of biomass or intraspecific competition on red salmon growth was of minor importance.

Although the type and concentration of fertilizers used increased organic production, no doubt more extensive experimentation would show that smaller amounts of various elements would do equally well. For example, during 1955 trace elements were added to jugs of Bare Lake water whereupon accelerated photosynthesis resulted from an extremely minute amount of material. The possibility exists that productivity might be increased in lakes by small, inexpensive additions of material.

SUMMARY

1. Spawning escapements entering Bare Lake, Alaska, have ranged from 52 to 551 salmon during the years 1950-56. During this period, the commercial catch of Bare Lake fish was small, except in 1950 and 1951.

2. Nine age groups of adult salmon have been found at Bare Lake. Of these the 5₂, 5₃, and 6₃ age groups are the most important.

3. The size at maturity of Bare Lake red salmon appears to be dependent upon sex and environmental conditions during the last year the fish spend in the ocean.

4. A predominance of female salmon occurred each year in the spawning escapement. It would seem a differential mortality in favor of the females exists during the marine period of life.

5. The fecundity of Bare Lake female red salmon is dependent mostly upon size at maturity.

6. Greater percentages of smolts migrate to sea at an earlier age from brood years of high smolt production than from brood years of low smolt production. Population pressure may cause this.

7. An increase in the size of smolts has not brought about an increase in the percentage of the younger smolts in the seaward migrations. Generally the older smolts migrate to sea earlier in the season than the younger smolts.

8. Fertilization of Bare Lake has been accompanied by increased growth of young red salmon during residence there.

9. A close relation was found between the growth of red salmon of various fresh-water ages and the gross rate of photosynthesis during peri-

ods which would be likely to influence the food supply.

10. The fresh-water survival rate of red salmon from the annual egg deposition (corrected for egg retention of spawners) to the smolt stage has averaged 2.96 percent (range 1.0 to 5.1 percent) for years 1950-53.

11. The increase in the size of smolts since fertilization has been followed by an increase in their survival at sea.

12. Limited studies were conducted on juvenile coho salmon, Dolly Varden charr, and the three-spine sticklebacks. Sticklebacks and cohos compete with young red salmon for a common food supply. Dolly Varden prey on the red salmon smolts.

13. Growth studies were conducted only on the threespine stickleback. It was found that this species, unlike red salmon, did not respond to fertilization by increased growth. Data were inadequate on juvenile coho salmon, threespine stickleback, and Dolly Varden charr to determine the effect of fertilization on survival.

14. Other factors, including population biomass, incidence of diseased red salmon, and water temperatures, had no influence on the growth of red salmon juveniles and smolts for the years 1950 through 1956.

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APPENDIX

APPENDIX TABLE 1.—Egg counts of red salmon sampled at the weir site, Bare Lake, Alaska, 1950 to 1956

Date fish collected	Fork length (cm.)	Weight (lb.)	Age group	Egg count		
				Right ovary	Left ovary	Total
June 24..... 1950	56.5	4.62	5 ₂	1,845	1,480	3,325
June 19..... 1951	58.0	4.00	5 ₂	1,961	1,891	3,852
July 2.....	44.5	2.19	5 ₃	999	950	1,949
June 16..... 1952	58.6	5.19	5 ₂	1,749	1,866	3,615
18.....	59.1	5.84	5 ₂	2,131	2,323	4,457
July 2.....	56.0	4.62	5 ₂	1,696	1,217	2,913
2.....	60.8	5.88	5 ₂	1,822	1,722	3,544
3.....	51.2	3.25	5 ₃	1,370	1,183	2,553
3.....	55.4	4.25	5 ₃	1,607	1,461	3,068
3.....	57.3	5.31	5 ₃	1,737	1,590	3,317
8.....	56.7	4.44	5 ₂	1,600	2,163	3,763
12.....	58.7	4.88	5 ₂	1,980	1,898	3,848
12.....	55.6	4.22	5 ₂	1,435	1,230	2,665
14.....	55.9	4.62	5 ₂	1,736	1,802	3,538
14.....	57.5	4.50	5 ₂	1,920	2,003	3,923
15.....	52.6	3.53	5 ₂	1,506	1,122	2,628
June 18..... 1953	54.2	4.12	5 ₃	1,521	1,536	3,057
18.....	53.5	4.28	5 ₃	1,457	1,441	2,898
18.....	56.3	4.72	5 ₃	2,051	1,593	3,644
21.....	60.2	5.31	5 ₃	1,862	1,613	3,475
23.....	57.3	5.40	5 ₃	1,635	1,786	3,421
25.....	55.3	4.22	5 ₃	1,268	965	2,233
25.....	57.1	5.40	5 ₃	1,569	1,655	3,254
25.....	57.4	5.29	5 ₃	2,014	1,417	3,431
25.....	57.2	6.39	5 ₃	2,195	1,669	3,864
June 10..... 1954	59.0	5.40	6 ₃	1,945	1,487	3,432
17.....	55.0	4.31	6 ₃	1,458	1,371	2,829
19.....	51.5	3.62	5 ₃	1,533	1,074	2,607
20.....	55.0	4.62	6 ₃	1,939	1,547	3,486
20.....	50.5	3.09	5 ₃	946	1,071	2,017
20.....	59.0	5.31	6 ₃	1,722	1,714	3,436
July 5.....	53.0	3.88	5 ₃	1,131	1,317	2,448
5.....	52.0	3.62	5 ₃	1,642	1,373	3,015
Aug. 4.....	59.0	5.31	5 ₃	1,384	1,310	2,644
June 15..... 1955	52.0	3.69	5 ₃	1,601	1,818	3,419
17.....	54.0	4.15	5 ₂	1,493	1,361	2,824
17.....	49.0	3.21	5 ₃	1,065	1,367	2,432
18.....	56.0	5.06	5 ₂	1,749	1,391	3,140
21.....	52.0	3.69	5 ₃	1,363	1,530	2,893
26.....	55.0	4.34	6 ₃	1,302	1,493	2,795
26.....	49.5	3.31	5 ₃	1,262	1,150	2,412
27.....	55.5	3.88	6 ₃	1,607	1,435	3,042
July 1.....	51.0	3.47	5 ₃	1,498	1,386	2,884
1.....	57.0	4.94	5 ₂	1,828	1,562	3,390
1.....	51.5	3.88	5 ₃	1,603	1,423	3,026
1.....	51.0	4.78	5 ₃	1,843	1,586	3,429
3.....	55.5	4.40	5 ₂	1,922	1,355	3,277
6.....	52.0	3.72	4 ₂	1,631	1,413	3,044
6.....	51.5	3.62	5 ₃	1,411	1,300	2,711
11.....	53.0	3.81	5 ₂	1,394	1,122	2,516
June 11..... 1956	57.0	5.25	5 ₂	1,642	1,644	3,286
July 3.....	54.0	4.62	5 ₂	1,624	1,622	3,246
14.....	47.0	3.62	5 ₂	1,632	1,040	2,672

APPENDIX TABLE 2.—Migration, percentage age composition, mean fork length, mean weight, and sample size of red salmon smolts, by weeks, Bare Lake, Alaska, 1950 to 1956

Week ending	Weekly migration ¹	2-year-old smolts			3-year-old smolts			4-year-old smolts			Sample size
		Percent	Mean length (mm.)	Mean weight (gm.)	Percent	Mean length (mm.)	Mean weight (gm.)	Percent	Mean length (mm.)	Mean weight (gm.)	
1950											
May 31	707	24.2	70.9	3.26	74.4	78.4	4.31	1.4	92.5	7.67	97
June 7	5,530	63.1	70.8	2.92	36.9	78.0	3.91				503
14	1,936	86.4	70.4	2.96	13.6	78.6	4.05				225
21	1,001	82.3	71.0	3.18	17.7	77.0	3.93				98
28	690	82.6	71.0	3.17	17.4	79.0	4.15				25
July 5	181	39.2	75.2	4.24	60.8	77.9	4.68				21
12	117	28.2			71.8						
July 19-Aug. 9	237										
1951											
May 31	439	0			100.0	87.2	5.71				78
June 7	1,688	2.5	69.6	3.36	96.7	86.0	5.31	.8	96.8	7.89	439
14	1,241	6.0	69.4	3.44	93.2	85.9	5.24	.8	102.0	8.87	365
21	174	42.0	71.2	3.19	57.4	87.2	5.57	.6	105.0	10.01	191
28	511	83.4	69.2	2.96	16.2	86.2	5.47	.4	104.0	10.12	303
July 5	294	94.6	68.8	2.97	5.4	84.1	5.83				318
12	142	91.5	69.7	3.15	8.5	80.1	4.78				138
July 19-Aug. 16	14	100.0			0						
1952											
May 24	3	0			100.0	90.3	6.42				4
31	328	7.0	79.6	4.38	90.5	88.1	6.12	2.5	102.2	9.52	209
June 7	1,664	12.0	78.7	4.09	87.4	85.5	5.45	.6	96.3	7.82	488
14	2,646	13.2	75.2	3.65	83.8	82.0	4.77	3.0	100.1	8.74	485
21	1,383	36.0	75.5	3.75	62.1	82.0	4.75	1.9	101.3	9.29	421
28	1,400	80.0	74.3	3.50	19.2	79.7	4.27				448
July 5	636	95.1	75.4	3.79	4.9	81.0	4.72				361
12	396	94.9	77.1	4.16	5.1	83.1	5.07				274
19	107	94.4	78.7	4.57	5.6	85.8	5.93				94
26	50	95.0	81.1	4.99	2.0	97.0	9.15				36
Aug. 2	7	100.0									
9	2	100.0									
1953											
May 24	26	0			100.0	93.9	7.20				11
31	1,104	7.5	81.7	4.62	92.3	93.4	7.08	.2	109.0	11.35	435
June 7	1,377	9.3	81.4	4.76	90.7	94.0	7.27				409
14	911	40.8	82.3	4.96	59.2	92.4	6.99				404
21	900	49.8	82.9	5.03	50.2	93.1	6.99				370
28	612	78.9	84.4	5.56	20.4	94.6	7.81	.7	113.0	13.45	298
July 5	135	87.4	87.5	6.36	12.6	96.6	8.33				135
12	3	66.7	88.5	6.72	33.3	94.0	8.24				3
1954³											
May 24	36	83.3	69.0	2.77	16.7	99.0	8.13				13
31	135	76.2	70.3	2.96	32.8	97.1	8.34	.7	116.0	13.17	79
June 7	202	2.5	79.4	5.08	90.1	104.5	10.65	7.4	125.9	19.85	138
14	673	9.5	81.0	5.13	87.4	102.9	9.95	3.1	131.6	21.79	309
21	908	56.2	84.5	5.82	42.7	104.0	10.67	1.1	132.5	22.28	297
28	1,225	88.9	88.5	6.92	13.1	104.2	11.12				304
July 5	3,697	96.5	92.1	7.82	3.5	109.4	13.15				489
12	3,524	97.2	92.8	7.89	2.8	115.5	15.30				443
19	770	99.1	94.0	8.00	.9	115.5	15.25				163
26	134	100.0	94.6	8.07	0						65
Aug. 2	837	95.0	98.6	9.25	4.5	129.0	21.22				149
9-23	48	93.8	100.5	9.70	6.2	119.0	16.82				42
1955⁴											
May 24	13	15.4			84.6						
31	119	13.4	81.1	4.19	84.9	103.1	9.96	1.7	124.0	17.94	106
June 7	6	0			100.0						
14	307	7.2	88.0	8.16	88.3	107.5	11.94	4.5	133.8	23.40	99
21	6,169	46.8	89.2	6.65	50.4	106.8	11.68	2.0	136.6	25.18	457
28	8,131	92.0	89.3	6.44	7.0	105.4	11.13	1.0	141.9	27.53	470
July 5	3,055	97.2	91.9	7.30	2.2	111.3	13.67				687
12	3,055	99.1	99.2	9.54	.9	114.6	15.25				514
19	1,488	98.9	105.0	11.38	.9	119.2	18.00				348
26	1,637	97.1	107.6	11.98	2.9	122.5	18.44				185
Aug. 2	52	96.2			3.8						
9-30	2	100.0			0						
1956											
May 31	311	22.5	79.6	4.10	77.5	109.2	11.20				314
June 7	2,464	20.8	80.8	4.32	78.9	108.9	10.92	.3	132.5	20.22	728
14	2,440	48.6	79.9	4.20	50.1	108.0	10.55	1.3	137.0	22.93	596
21	195	79.0	82.2	4.66	19.5	109.2	11.04	1.5	141.3	25.17	197
28	349	96.8	83.1	4.99	3.2	107.1	10.32				350
July 5	77	96.1	87.3	6.25	3.9	111.0	12.05				76
12	539	98.9	89.9	8.85	1.1	110.2	12.25				381
19	145	98.6	90.4	8.84	1.4	110.0	12.63				142
26	3	100.0									
Aug. 2-30	2	100.0									

¹ Smolt mortalities at the weir are not included.² Fry; migrating in their first year.³ Not included in the table are six 5-year-old smolts (1 taken in 1954, length 144 mm., 5 taken in 1955, mean length 157.4 mm.).

APPENDIX TABLE 3.—*Each seine catches, Bare Lake, Alaska, 1950-56*
[Area of catch: 1—South end of lake; 2—North end of lake]

Date	Area of catch	Number of hauls	Red salmon juveniles	Stickleback	Coho salmon juveniles	Dolly Varden charr
1950						
Aug. 15	2	1	130	855	1	2
25	2	1	100	585	3	9
31	2	1	130	516	1	1
1951						
June 13	2	1	60	423	2	9
29	2	1	21	638	7	8
July 8	1	1	27	1,002	1	0
22	1	2	58	348	5	4
Aug. 7	1	1	147	146	8	6
25	1	1	171	406	16	3
Sept. 12	1	1	176	156	21	6
1952						
May 19	2	1	103	1,153	25	7
25	1	4	56	1,008	11	7
June 8	1	1	23	86	6	4
8	1	1	103	358	11	0
29	1	2	76	62	4	2
Aug. 1	2	1	41	1,752	14	4
6	2	1	20	768	22	12
Sept. 11	1	2	88	51	25	5
1953						
May 23	1	1	123	171	35	2
June 8	1	1	171	1,688	23	1
27	1	1	21	2,082	19	0
27	1	1	60	3,863	5	0
July 11	1	2	75	1,566	16	0
24	1	1	46	1,547	10	0
Aug. 12	1	1	288	411	8	0
29	1	1	98	207	19	1
Sept. 3	1	1	94	27	9	2
3	2	1	774	1,120	25	6
4	2	1	148	595	26	20
8	2	1	176	1,246	22	2
9	2	2	324	942	30	7
9	1	1	52	54	7	0
10	2	1	127	619	26	5
Oct. 1	1	1	46	0	7	0
1954						
May 24	1	1	122	83	22	1
June 7	1	1	90	944	10	2
24	2	1	218	2,605	14	72
24	1	1	51	291	1	2
26	1	1	251	302	7	0
26	2	1	29	4,075	3	30
July 12	1	1	372	663	35	0
24	2	1	278	1,700	0	0
24	2	2	114	37	27	8
26	1	1	321	1,100	32	12
29	1	1	461	1,500	4	1
29	2	1	275	1,500	8	0
Aug. 7	1	1	109	1,500	17	9
7	2	1	90	1,000	7	7
9	2	1	970	707	6	2
10	1	1	229	1,500	4	17
14	2	2	34	1,500	1	4
17	1	2	76	276	8	2
27	1	1	364	1,500	1	12
29	2	2	230	167	6	28
Sept. 30	2	2	0	1,400	0	0
5	2	1	0	1,200	0	0
6	1	1	36	250	3	0
28	1	1				
1955						
May 23	1	1	128	1,288	49	2
June 7	1	1	130	377	0	1
24	1	1	74	607	3	6
July 12	1	1	102	986	8	7
18	1	1	190	346	10	15
30	1	1	172	17	3	2
Aug. 10	1	1	132	164	26	4
17	1	1	72	85	8	5
18	1	1	72	807	1	1
19	2	1	92	2,043	9	0
20	2	1	24	674	3	1
27	1	1	94	155	27	7
Sept. 6	1	1	70	1,370	11	1
26	1	1	42	37	4	3
26	2	1	2	26	1	1
1956						
May 30	1	2	17	533	11	0
June 20	1	2	7	1,007	13	5
July 10	1	1	44	364	12	10
23	1	2	602	452	22	1
Aug. 4	1	1	185	200	21	11
16	1	1	197	99	6	2
28	1	1	60	171	7	0

1 Estimated catch.

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

CHANGES IN TUNA LANDINGS OF THE HAWAIIAN LONGLINE FISHERY 1948-1956

BY RICHARD S. SHOMURA



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ABSTRACT

This study was undertaken to determine the cause of a change in species dominance in the catch of the Hawaiian longline fishery from yellowfin (*Neothunnus macropterus*) to bigeye tuna (*Parathunnus sibi*) during the period 1948-49. The available commercial catch records showed that the reversal in species resulted from a shift by the larger vessels of the fleet from fishing grounds in the leeward waters of the northern islands to grounds located in the windward waters of the southern islands. Bigeye tuna are more available to the fishery in the windward waters than in the leeward, whereas the yellowfin tuna are taken in greater numbers in the leeward areas. The bigeye season extends from October through May, whereas the best yellowfin catches are made during the summer months, June through August.

A hypothesis is given to explain the distribution and migration of the bigeye tuna in the central Pacific. Essentially, it postulates spawning in the tropical waters south of the Hawaiian Islands, a migration of young fish northward, a seasonal north-south movement of the adult population, and finally a continued southward movement to the tropical spawning grounds by adults in imminent spawning condition.

CHANGES IN TUNA LANDINGS OF THE HAWAIIAN LONGLINE FISHERY, 1948-1956

By RICHARD S. SHOMURA, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

The Pacific Oceanic Fishery Investigations¹ (POFI) of the U.S. Fish and Wildlife Service has studied the hydrography and productivity of the central Pacific Ocean and has carried out exploratory fishing cruises to encourage the maximum development and utilization of the high-seas fishery resources of this area.

One segment of POFI's task has been to gain an understanding of the nature and problems of the existing commercial fisheries in the central Pacific. Although small quantities of tuna are taken in Hawaiian waters by trolling and handline, the two major fisheries in the islands are the pole-and-line fishery for skipjack (June 1951, Yamashita 1958) and the longline (flagline) fishery (June 1950, Otsu 1954) for the larger subsurface tunas. In a good year (1951) the skipjack fishery landed 12,900,000 pounds with a value of \$1,700,000 (Yamashita 1958). The longline fishery in 1952, a good year for that fishery, landed tunas and marlins totaling 4 million pounds and valued at \$1,200,000 (Otsu 1954). Though these fisheries are small in respect to total landings, their strategic occurrence in midocean makes them ideal laboratories for the study of certain problems concerning midocean tunas.

The present study of the Hawaiian longline fishery was stimulated by Otsu's (1954) finding that from 1946 to 1952 there was a decline in landings of yellowfin (*Neothunnus macropterus*) and an increase in landings of bigeye (*Parathunnus sibi*), with the reversal in dominance between 1948 and 1949. The change in the bigeye landings is especially noteworthy since it involved an increase from 12,000 pounds in 1946 to 2,200,000 pounds in 1952, without a corresponding increase

in the overall fishing effort as indicated by the total number of trips (Otsu 1954). The purpose of the present study was to describe the seasonal and long-term trends in the landings of the two species, and if possible, to determine cause of the fluctuations.

The basic catch data utilized in this report were supplied by the Hawaiian Division of Fish and Game, through the courtesy of Director Vernon E. Brock. T. Shimizu of the Division's staff helped to assemble the data for analysis. The longline fishermen provided valuable information on the fishery and personnel of the auction firms, Kyodo Fishing Co., United Fishing Agency, and Hawaii Fishing Co., made auction records available.

DESCRIPTION OF THE FISHERY

The Hawaiian longline fishery is the only American commercial fishery utilizing the longline method, as developed by the Japanese (Shapiro 1950), to capture subsurface tunas. The history and recent status of the fishery in Hawaii have been described by Brock (1949), June (1950), and Otsu (1954).

The longline fishery is dependent on vessels located at various ports throughout the Hawaiian Islands chain; however, the two major fleets are based at Hilo, Hawaii, about 10 vessels, and at Honolulu, Oahu, 31 to 33 vessels (Otsu 1954). These vessels range from 28 to 62 feet in length and are constructed along lines similar to the sampans used in the pole-and-line fishery (June 1951). They have a high, narrow bow with the wheelhouse and sleeping quarters located forward, leaving a spacious afterdeck of low freeboard. The latter facilitates the landing of large fish which, in the case of the marlins, occasionally exceed 1,000 pounds in weight. The vessels are

¹ Redesignated Bureau of Commercial Fisheries Laboratory, January 1, 1959.

NOTE.—Approved for publication, July 1, 1958. Fishery Bulletin 160.

generally powered by high-speed diesel engines, and since they lack mechanical refrigeration systems the catch is stored in crushed ice.

The longline is made up of a number of units of gear called baskets which are joined in a series and allowed to drift free of the vessel (June 1950). Each basket of gear is composed of a cotton mainline section from which are suspended 4 to 6 branch lines each bearing a single hook. The longline is supported at the surface by wooden, glass, or metal floats. The number of baskets fished per day varies with the individual vessel but rarely does it exceed 40 baskets. By comparison, Japanese fishermen operating on a considerably larger scale may use more than 300 baskets of gear per set (Ego and Otsu, 1952).

The average length of a trip for a Honolulu-based vessel is 8 or 9 days and a majority of the trips are made within sight of land. The gear is set in the morning and retrieved in the afternoon. During the intervening period the line is patrolled and, if the fishermen are able to recognize the presence of a hooked fish by a submerged buoy, the fish is landed and the hook reset.

Composition of the longline catch is varied and consists of a number of species of tunas and spearfishes. In addition to bigeye and yellowfin, the tuna catch includes small numbers of albacore (*Germo alabunga*), skipjack (*Katsuwonus pelamis*), and on rare occasions bluefin tuna (*Thunnus orientalis*). Among the spearfishes the most commonly taken species are the striped marlin (*Makaira audax*) and black marlin (*Makaira ampla*),² while lesser numbers of white marlin (*Istiompax marlina*),³ broadbill swordfish (*Xiphias gladius*), and shortnose spearfish (*Tetrapturus angustirostris*) are taken. Other species caught on the longline include the dolphin (*Coryphaena hippurus*), wahoo (*Acanthocybium solandri*), and various species of shark. Because of the wide variety of species taken and different periods of seasonal abundance, the fishery is capable of year-round operation.

MATERIALS AND METHODS

The basic data used in this study were derived from fish catch reports submitted by members of the fishing industry to the Hawaiian Division of

Fish and Game. The form of this report used in the longline fishery has undergone several modifications; a sample of the present form is shown in appendix figure 1, page 105. The areas fished were reported in code numbers indicated on a fisheries chart (app. fig. 2). The reported data were compared with records kept by the auctioning firms and some adjustments made, especially for the early years when individual boat owners filled in the fish catch reports, for they occasionally combined the catches of several trips and reported them as a single trip. Also, the yellowfin and bigeye catches often were not separated according to species, but were combined in one or the other species category. In recent years the auction firms have filled out the forms after obtaining the essential data from the fishermen.

In addition to the sources given, more detailed information was obtained from 1949 to 1952 by interviewing vessel captains. These data formed the basis of Otsu's (1954) study and have also been utilized in this report.

Preliminary examination of the data showed that for an accurate evaluation of the fishery some selection of data would be necessary. Description of the method used follows.

SELECTION OF FLEET AND VESSELS

Initially, the study was limited to the Honolulu-based fleet, because the landings from this fleet comprised more than 80 percent of the total Hawaiian longline landings and accessibility of the Honolulu auctioning records made it possible to check doubtful data. Limiting the study to the Honolulu fleet does not imply that the fishing area was proportionately restricted, since the larger vessels at least fished throughout the major Hawaiian Islands group.

It was also decided to limit the sampling to vessels operating 5 or more of the 9 years under consideration. This eliminated recent additions to the fleet, which were known to fish for longer periods and with more units of gear than the older vessels. Evidence that the bulk of the fleet was the same throughout the period 1948 to 1956 is indicated by the operation during 1956 of 23 of the total of 31 vessels comprising the 1948 fleet. This stability is in part a reflection of the short period under study and the fact that most of the vessels were comparatively new. Of the 39 vessels

² Called blue marlin by continental Americans.

³ Called black marlin by continental Americans.

fishing from 1948 to 1956, 21, or more than half of the total were launched during 1946 or 1947.

SEPARATION OF FLEET BY SIZE OF VESSEL

Otsu (1954) stated that some of the Honolulu-based longline vessels fished in waters around Oahu continuously throughout the year while others roamed the entire area, fishing as far as the northeastern shore of the island of Hawaii (fig. 1). The records showed that vessels fishing exclusively around Oahu were smaller in size (registered length⁴ of 45 feet or less) and fished fewer units of gear and fewer days per trip. Accordingly the vessels were classed, based on our knowledge of the fishery, as small or large and the catch data for each class were treated separately.

THE TRIP AS A MEASURE OF EFFORT

Longline catch data have ordinarily been presented in terms of catch per 100 hooks (Murphy

⁴ The vessel lengths were obtained from Annual Merchant Vessels of the United States, compiled by the U.S. Treasury Department.

and Shomura, 1953). For the Hawaiian fishery, some data are available on the number of boat-days and the number of baskets fished in the early years, 1949 to 1952 (Otsu 1954), and for the years subsequent to 1955 the revised fish catch report includes the number of days at sea (app. fig. 1, p. 105). For the intervening years, 1953 to 1955, no such measures of effort are available. Even for the earlier period, 1949 to 1952, the data on the number of days fished are inadequate for a comprehensive study.

The only measure of fishing effort available for the entire period, 1948-56, is the number of trips. Thus, through necessity, the catch per unit of effort must be based on the catch per trip. To justify the trip as a measure of effort it was necessary first to determine whether there had been any changes in the length of trip during the period. Before 1952-53 some data were available on the number of days fished per trip, whereas for the subsequent years data were available on

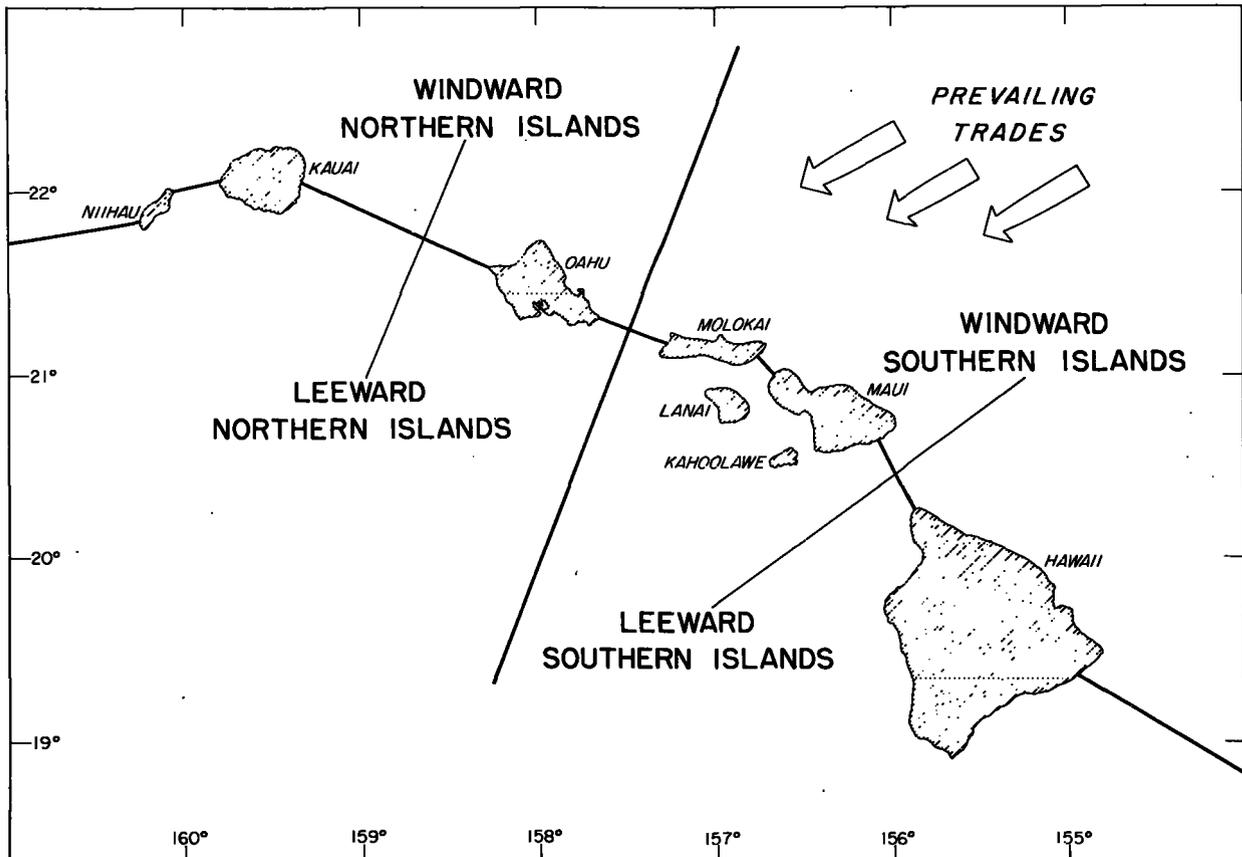


FIGURE 1.—Chart of the major Hawaiian Islands subdivided into windward and leeward zones for areal studies of catch.

the number of days at sea. Excluding weather as a factor, these two measures are essentially the same for the small vessels. These vessels generally fish in the immediate vicinity of Oahu and are thus able to return to port the night of the last fishing operation. On the other hand, if the large vessels fish in the windward areas of the

southern islands, they must travel from 120 to 200 miles from the fishing grounds to Honolulu. This introduces a possible differences of at least 1 day, depending on the area fished, between the number of days fished and the number of days at sea. Table 1 gives the average number of days of fishing per trip for small and large vessels (the latter

TABLE 1.—Number of days fished per trip, by size of vessel, 1949 to 1956

[Vessels selected]

	1949-50	1950-51	1951-52	1952-53	1953-54	1954-55	1955-56
Small vessels (<45 feet):							
Number of trips.....	41	52	47	107	88	201	183
Average number of days fished per trip.....	8.3	8.2	8.4	8.0	7.9	7.7	8.4
Large vessels (>45 feet):							
Number of trips.....	125	132	165	165	178	321	316
Average number of days fished per trip.....	9.7	9.0	8.4	8.6	9.2	9.4	9.3

adjusted for traveling time). There are no evident trends in length of trip for either vessel category. For the small vessels the average trip ranged from a low of 7.7 days during 1954-55 to a high of 8.4 days in both 1951-52 and 1955-56, with an overall average of 8.1 days for the entire period. For the large vessels, the number of days fished per trip (adjusted) ranged from a low of 8.4 days during 1951-52 to a high of 9.7 days for 1949-50. The overall average length of trip for the entire period for the large vessels was 9.1 days.

Another factor that should be considered in this evaluation of fishing effort is the number of baskets fished per day. As mentioned previously, the amount of gear fished per day was related to the size of the vessels, the larger vessels fishing more baskets of gear than the smaller. This difference is reduced in importance by the separation of the fleet into the two size categories. Some data are available on the number of baskets fished per day for the years 1950, 1952, and 1955 (table 2). There is some evidence that 1952 was an

TABLE 2.—Number of baskets of gear fished per day, by size of vessel

[Vessels selected]

	1950	1952	1955
Small vessels (<45 feet):			
Number of vessels.....	8	12	7
Average number of baskets fished per day.....	26	24	26
Range (baskets).....	22-30	21-31	20-30
Large vessels (>45 feet):			
Number of vessels.....	17	18	16
Average number of baskets fished per day.....	30	28	31
Range (baskets).....	21-36	25-32	24-35

atypical year (Otsu 1954). If this year is omitted and only 1950 and 1955 considered, it appears that the number of baskets fished per day did not change materially for either the small or the large vessels. In both years the small vessels fished an average of 26 baskets of gear per day, whereas the large vessels increased the amount of gear fished per day from 30 baskets in 1950 to 31 baskets in 1955.

A final test of the trip as a measure of fishing effort is afforded by a comparison of the catch per trip with the catch per 100 hooks in those periods for which both kinds of data are available. Unfortunately, however, the only year with adequate data was 1952, which has been considered atypical. Nevertheless, a plot (fig. 2) of these two units shows that the two variables are

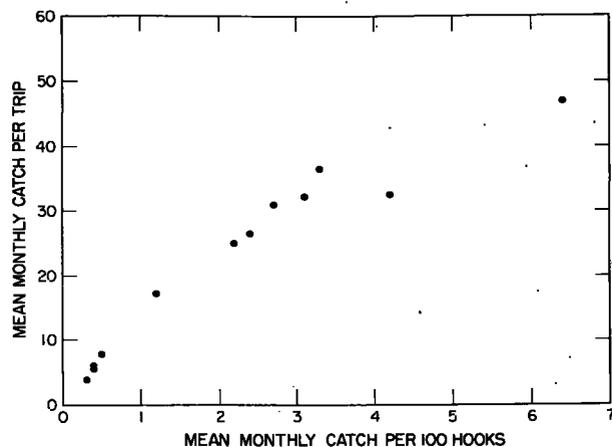


FIGURE 2.—Comparison of monthly mean bigeye catch per 100 hooks and per trip in 1952.

closely correlated and exhibit a linear relation. We believe, therefore, that the catch per trip is the best attainable measure of availability of the two species of tuna to longline gear.

ANALYSIS OF THE DATA

The total Hawaiian landings of bigeye and yellowfin, shown in figure 3,⁵ include catches made by various methods of tuna fishing, e. g., the longline, pole-and-line, trolling, and handline fishing. The yellowfin catch has shown a steady decline from 1,325,000 pounds in 1946 to 446,000 pounds in 1955, whereas the bigeye catch increased from a low of 199,000 pounds during the 1946-47 season to a high of 2,710,000 pounds for the 1953-54 season. Since 99 percent of the bigeye and about 85 percent of the yellowfin are caught in the longline fishery, the longline landings parallel the total landings.

The trend in yellowfin landings of the Honolulu-based vessels shows some divergence from the trends in the total catch by all methods and in the total longline landings (fig. 3). Despite the steady decline observed in the overall catch, the yellowfin landings of the Honolulu fleet remained at a relatively stable level, averaging 375,000 pounds annually from 1948 through 1952. Then in the 3 years that followed, 1953 to 1955, the Honolulu landings dropped 30 percent to an average annual figure of 275,000 pounds. Even this drop failed to keep pace with the decline of the overall catch, with the result that the Honolulu landings, which in 1948 and 1949 made up only 36 and 38 percent of the total yellowfin catch of the longline fishery, averaged 64 percent during the next 6 years, 1950 through 1955. This failure of the trend in the Honolulu yellowfin landings to parallel that for the Territory as a whole cannot be fully explained at present; it appears to be associated with operational aspects of the fishery to be discussed later in this report. It should be mentioned, however, that while the data for the Honolulu fleet have been checked and corrected by means of various sources, the same has not been done for the remaining Hawaiian longline data.

⁵Since the bigeye season occurs in the winter and spring months, the annual period for bigeye extends from July of one year through June of the following year. For yellowfin the calendar year is retained, inasmuch as the yellowfin landings reach a peak during the summer months.

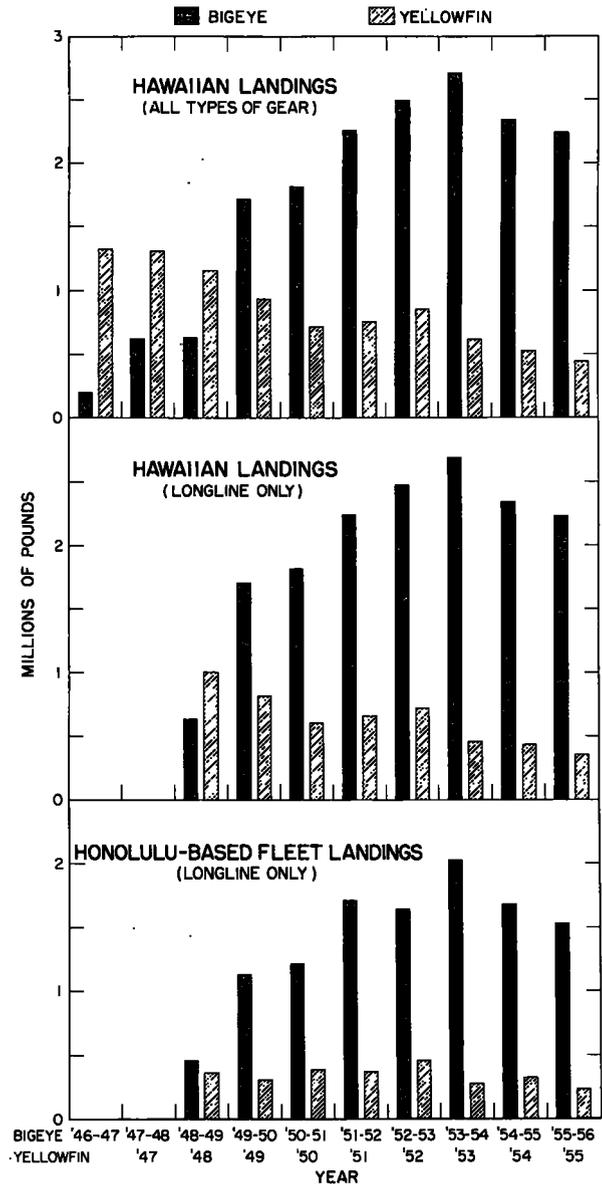


FIGURE 3.—Landings of bigeye (by fiscal year) and yellowfin (by calendar year), 1946 to 1956. (See appendix table 1.)

CATCH STATISTICS

Unless otherwise stated, the following discussions on landings and catch rates are in terms of numbers of fish rather than weight.

The bigeye catch of the selected large vessels varied directly with the landings of the entire Honolulu fleet, with a 300-percent increase between 1948-49 and 1953-54 and a decline thereafter (fig. 4). In contrast, the catch of the small

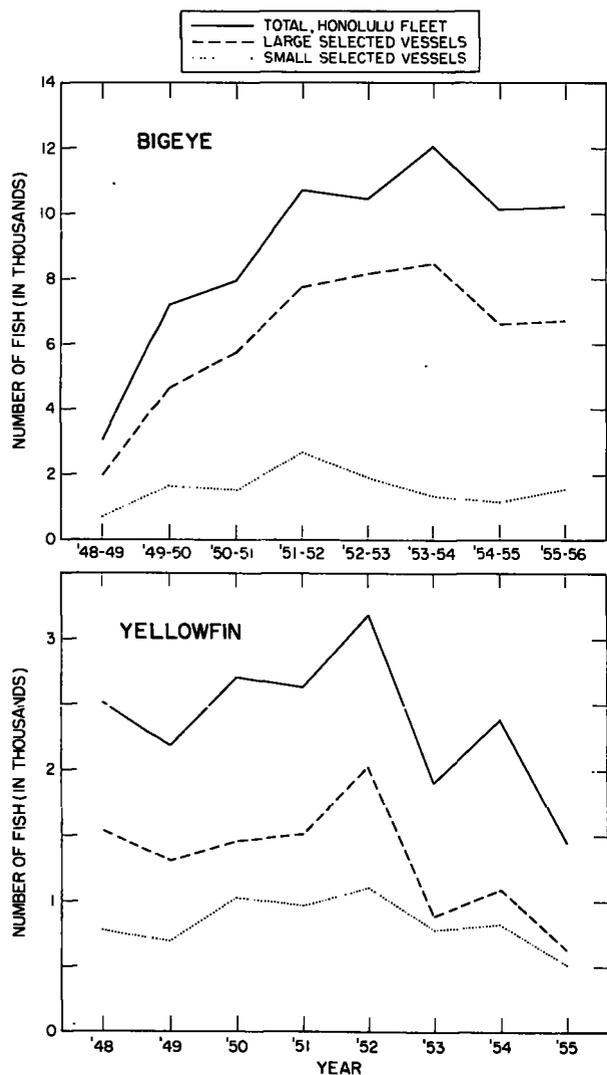


FIGURE 4.—Bigeye catch (by fiscal year) and yellowfin catch (by calendar year), by size of vessel.

selected vessels showed a slight rise from 1948-49 to 1951-52 and a decline thereafter. Thus, it appears that the tremendous increase in overall production was contributed by the large vessels.

The yellowfin landings, likewise, suggest that changes in the total catch were caused by changes in the landings of large vessels only. The most distinctive feature of the yellowfin landings (fig. 4) is the shift in relative proportion of the total catch obtained by the two classes of vessels. The proportion of the total yellowfin catch taken by the larger vessels was much higher before 1953

than it was during the last 3 years of the study, 1953 through 1955. Since this shift was coincident with the increased bigeye catches of the large vessels, it is evident that the changes in landings are related to factors affecting only the large vessels.

FISHING EFFORT

Examination of the number of baskets fished per day and the number of days per trip indicated only slight variations in these measures of effort; thus, any substantial changes in the overall effort, if they did occur within the Honolulu fleet, should be revealed in the number of trips made each year. Figure 5 shows that there was a steady increase in the total number of trips from 1948-49 to 1953-54 and a decline in the last two seasons 1954-55 and 1955-56. The increase was the result of more trips being made per boat, as shown by the higher number of trips per boat-month (fig. 5), and also the result of more vessels being added than were lost to the fleet. The latter is indicated in table 3 by the increased number of trips of the nonselected vessels, which presumably were recent additions.

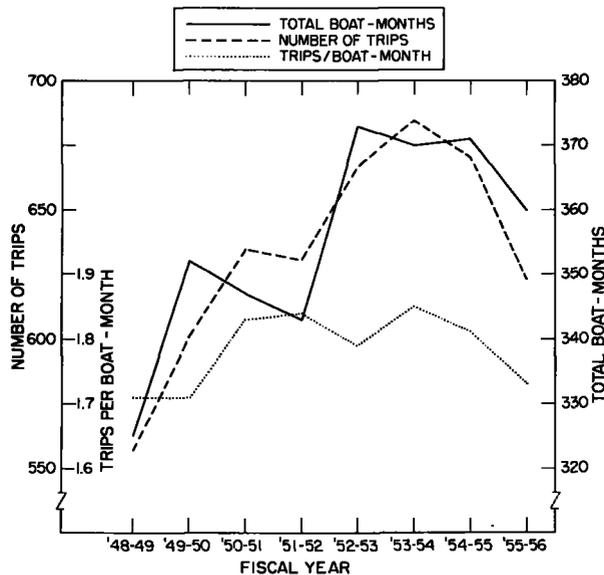


FIGURE 5.—Trends in fishing effort of Honolulu-based fleet, 1948-49 to 1955-56.

In a comparison of the effort expended (fig. 6) we find that both the small and large selected vessels followed the trend of the entire fleet.

TABLE 3.—Effort expended by Honolulu-based fleet, 1948-49 to 1955-56

Measure of effort	1948-49	1949-50	1950-51	1951-52	1952-53	1953-54	1954-55	1955-56
Boat-months:								
Selected small vessels.....	105	119	119	136	141	108	111	100
Selected large vessels.....	186	195	196	199	213	207	199	194
Total.....	291	314	315	335	354	315	310	294
Nonselected small vessels.....	4	4	5	1	12	12	12	12
Nonselected large vessels.....	30	34	27	7	7	43	49	54
Total.....	34	38	32	8	19	55	61	66
Trips:								
Selected small vessels.....	197	215	236	263	264	218	219	193
Selected large vessels.....	309	327	344	354	374	370	344	323
Total.....	506	542	580	617	638	588	563	516
Nonselected small vessels.....	4	6	8	2	19	24	27	19
Nonselected large vessels.....	47	53	46	12	10	73	81	88
Total.....	51	59	54	14	29	97	108	107
Trips per boat-month:								
Selected small vessels.....	1.88	1.81	1.98	1.93	1.87	2.02	1.97	1.93
Selected large vessels.....	1.67	1.68	1.76	1.78	1.76	1.79	1.73	1.66

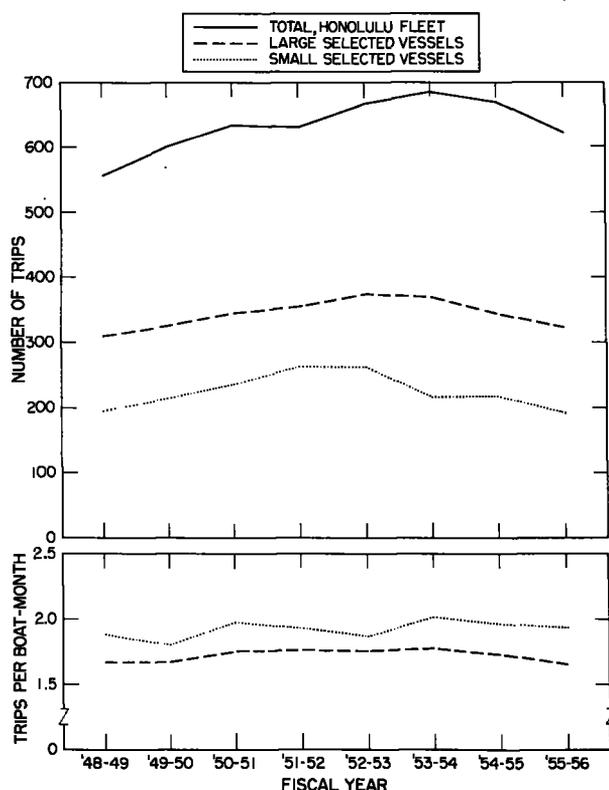


FIGURE 6.—Trends in fishing effort of small and large vessels, 1948-49 to 1955-56.

CATCH PER UNIT OF EFFORT

The marked seasonal variation in catch per unit of effort for the bigeye and yellowfin tuna is shown in figure 7. The peak catch of yellowfin occurred during the summer and of bigeye during

the winter and spring months. Of interest is the difference in catch rate for the two species in relation to size of vessel. The bigeye catch of the large vessels was considerably higher than that of the small vessels, the difference being more evident during the later years. On the other hand, with respect to yellowfin, the large and small vessel catch rates were nearly equal, the large vessels having only a slightly higher average catch.

The increase in bigeye catches and the difference in relative fishing success by vessel size for the two species can be better illustrated by the average annual catch rates (fig. 8). The large vessels experienced a sharp increase from 6.5 bigeye per trip during the 1948-49 season to 21.9 during the 1951-52 season, an increase of about 240 percent. The catch rates in subsequent years were stable at this high level, with only a slight decrease during the last two seasons, 1954-55 and 1955-56. The small vessels, on the other hand, exhibited minor fluctuations in the bigeye catch rate during the eight seasons, but the catch remained at a relatively low level.

The yellowfin catch rates (fig. 8) varied irregularly. The small vessels had a stable yellowfin catch rate of three to four fish per trip from 1948 through 1954 and a noticeable decline in 1955. On the other hand, the large vessels experienced two levels of fishing success. The first and higher level during 1948 through 1952, when the catches ranged from four to five yellowfin per trip, and the second and lower level persisting through the last three seasons, 1953 to 1956, with a catch rate

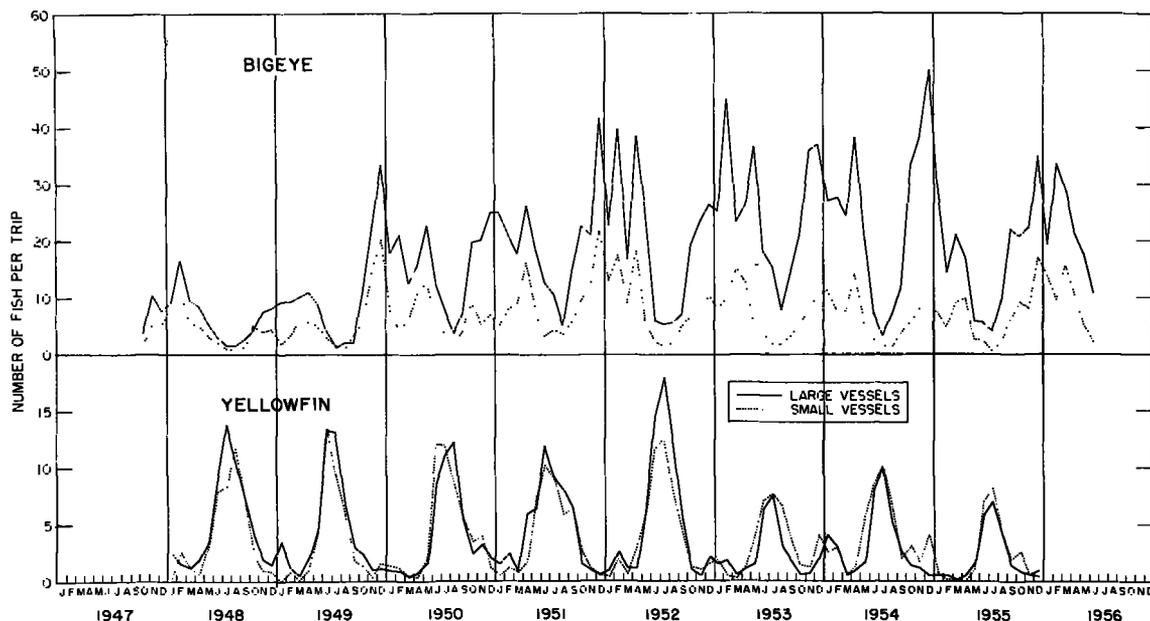
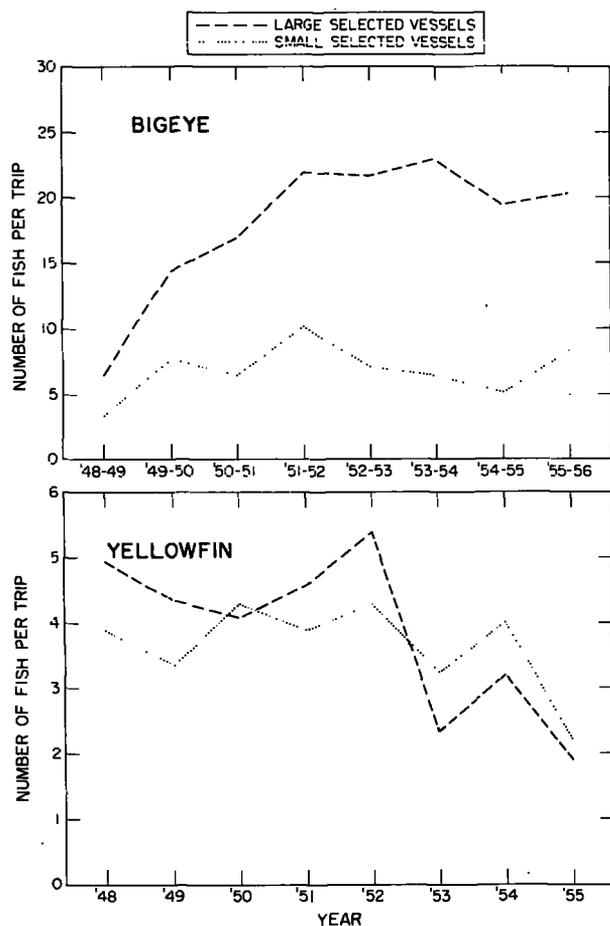


FIGURE 7.—Average catch per trip of bigeye and yellowfin tuna, by month and by vessel size.



of two to three yellowfin per trip. The most significant feature of this change in level is that for the last three seasons the catch rate of the large vessels was lower than that of the small vessels. This difference is surprising when it is realized that the large vessels fished more days per trip and more units of gear than did the small vessels.

Since the factors contributing to the trip as a measure of fishing effort have been analyzed and found to be stable, especially when vessel size has been adjusted, the discrepancies observed must be explained by changes in availability of the species, either by fluctuations in their actual abundance or indirectly by inherent differences in fishing success in the various areas fished. With regard to abundance, to explain the differences in bigeye catch by the two size groups of vessels would require an increase in the bigeye population which did not distribute itself uniformly throughout the fishing areas. This is possible, but improbable, when one must explain a simultaneous decrease in yellowfin abundance during the last three seasons—a decrease which would be confined only to the areas fished by the large vessels. The most probable explanation which satisfies all these varying points

FIGURE 8.—Average bigeye catch (by fiscal year) and yellowfin catch (by calendar year) per unit of effort, by size of vessel.

is a difference in availability of the two species among localities and an increased fishing effort by the large vessels in areas containing more bigeye.

CHANGES IN FISHING AREAS AND EFFORT

Because of a limited range, the Honolulu-based small vessels must confine their fishing to the immediate vicinity of Oahu. The distribution of their trips, by season and area, is given in table 4. Aside from a seasonal shift in effort, there appears to be no general change in fishing area within the period studied. More than 80 percent of the trips of these vessels were to the windward and leeward areas of Oahu, and of these the leeward areas received the greater effort. The small vessels fished almost exclusively in the leeward areas during the summer months, and although there is a noticeable increase in fishing effort in the windward areas during the fall, winter, and spring months, the greatest percentage of the

trips were made in the leeward waters at all seasons. The reason that the increase in effort was not more pronounced in the windward areas during the bigeye season may be that the small vessels prefer the calmer waters to leeward in spite of the greater availability of bigeye in the windward areas (Otsu 1954).

The distribution of trips by season and area for the large vessels is given in table 5. In general, these vessels tended to fish in the lee of the northern islands and on the windward side of the southern islands. During recent years there has been a pronounced shift in emphasis from the former to the latter area. With the exception of the winter of 1948-49, the majority of the fishing during the winter season has been in the windward areas of the southern islands. Also notable is the small yet consistent fishing effort in the windward areas of the northern islands, which could be in response to a greater availability of bigeye in these waters.

TABLE 4.—Percentage distribution of trips of small vessels, by season and area, 1947 to 1956

Season	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
Spring:										
Northern Islands:										
Windward Kauai.....				13	5	5	10			
Leeward Kauai.....		6	23			10				
Windward Oahu.....		32	12		5				62	6
Leeward Oahu.....		36	65	87	89	85	62	95	33	94
Southern Islands:										
Windward Maui-Molokai.....		6					3			
Leeward Maui-Molokai.....		17					24	5	4	
Windward Hawaii.....										
Leeward Hawaii.....		2								
Number of trips.....		47	52	54	57	20	29	22	24	16
Summer:										
Northern Islands:										
Windward Kauai.....				2	2	2				
Leeward Kauai.....		17	8			2				
Windward Oahu.....		4				4				
Leeward Oahu.....		76	92	98	95	88	100	100	100	
Southern Islands:										
Windward Maui-Molokai.....		2			3	4				
Leeward Maui-Molokai.....										
Windward Hawaii.....										
Leeward Hawaii.....										
Number of trips.....		46	48	60	60	51	27	27	26	
Fall:										
Northern Islands:										
Windward Kauai.....			2							
Leeward Kauai.....		12	9	2						
Windward Oahu.....		12	2			12	4	9	28	
Leeward Oahu.....		72	85	96	90	71	83	91	72	
Southern Islands:										
Windward Maui-Molokai.....		5	2	2	10	17				
Leeward Maui-Molokai.....							8			
Windward Hawaii.....										
Leeward Hawaii.....										
Number of trips.....		43	47	58	48	59	26	23	25	
Winter:										
Northern Islands:										
Windward Kauai.....		3	4	3						
Leeward Kauai.....	4	9	2							
Windward Oahu.....	24	14	8	3	12	14	8	28	58	
Leeward Oahu.....	44	71	86	76	69	73	76	58	42	
Southern Islands:										
Windward Maui-Molokai.....	20	3		15	19	11	12			
Leeward Maui-Molokai.....	8			2		2	4	12		
Windward Hawaii.....										
Leeward Hawaii.....										
Number of trips.....	25	35	51	59	26	44	25	24	19	

TABLE 5.—Percentage distribution of trips of large vessels, by season and area, 1947 to 1956

Season	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
Spring:										
Windward northern islands.....		20	3	28	41	2	19		26	5
Leeward northern islands.....		23	68	29	49	42	7		12	11
Windward southern islands.....		43	20	37	6	43	52	97	53	43
Leeward southern islands.....		14	3	6	4	12	21	3	9	41
Number of trips.....		70	68	86	81	81	42	35	34	37
Summer:										
Windward northern islands.....		10	18	12	43	25		3		
Leeward northern islands.....		61	75	56	36	53	10	28	17	
Windward southern islands.....		13	4	29	13	16	87	44	67	
Leeward southern islands.....		16	3	4	3	1	3	25	17	
Number of trips.....		69	71	84	67	89	39	32	36	
Fall:										
Windward northern islands.....		18	24	17	11	23				
Leeward northern islands.....		55	27	41	22	10				
Windward southern islands.....		18	48	41	67	65	95	97	98	
Leeward southern islands.....		9	1	1		1	5	3	2	
Number of trips.....		77	82	83	85	77	43	34	40	
Winter:										
Windward northern islands.....	21	24	24	14	24	19	2		14	
Leeward northern islands.....	15	44	17	11	10	6	7			
Windward southern islands.....	52	31	59	74	67	75	86	100	78	
Leeward southern islands.....	12	1	1	1			5		8	
Number of trips.....	66	68	75	76	72	53	42	32	37	

Of the four seasons, the spring distribution of fishing effort was the most erratic. Even during this season, however, the effort was concentrated in the leeward areas of the northern islands and in the windward areas of the southern islands. In the earlier years, effort during the summer was concentrated in the leeward waters of the northern islands, but during the last three summers, 1953 through 1955, it noticeably declined.

The annual effort and catch of bigeye and yellowfin by the large vessels in the windward areas of the southern islands are summarized in figure 9. The effort increased from a low of 22 percent of the total annual trips made into this area during 1948-49 to a high of 88 percent during the 1953-54 season. The following two seasons showed a slight decline. Again the significant feature both of the bigeye and of the yellowfin catch is the position of each relative to the effort expended. It is evident that bigeye fishing was more successful in this area than elsewhere, judged by the consistently higher catch percentage, than would be expected from the amount of effort expended. On the other hand, the reverse is true for yellowfin, with the catch consistently lower than the effort expended, indicating that the area is not as good a fishing ground for yellowfin as for bigeye. From this it can be deduced that yellowfin are relatively more abundant in the leeward waters of the northern islands than in the windward waters of the southern islands.

The seasonal breakdown of catch and fishing effort for the windward areas of the southern islands is presented in figure 10. The bigeye and

yellowfin catch and effort by season still follow the yearly trends. For all four seasons, the bigeye catch is consistently higher than expected from

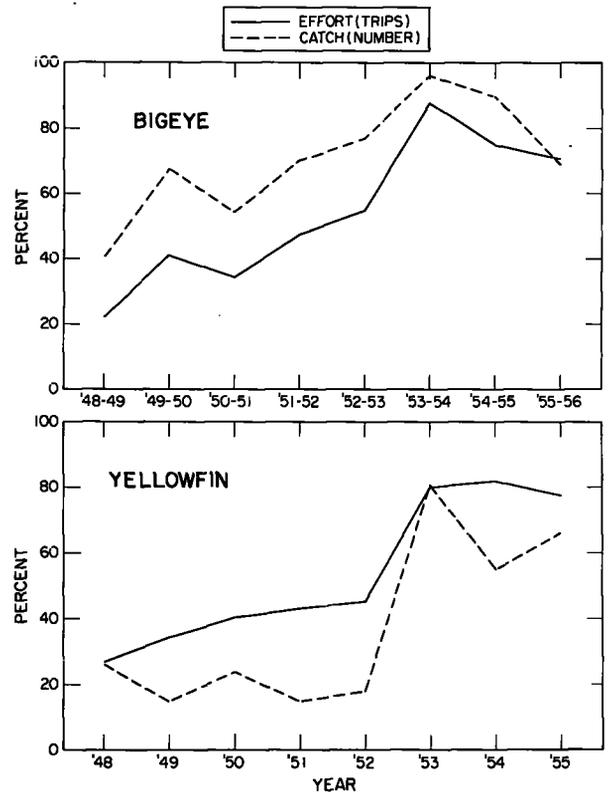


FIGURE 9.—Catch of bigeye (by fiscal year) and yellowfin (by calendar year) in respect to effort of large vessels in windward waters of the southern islands. (See appendix table 2.)

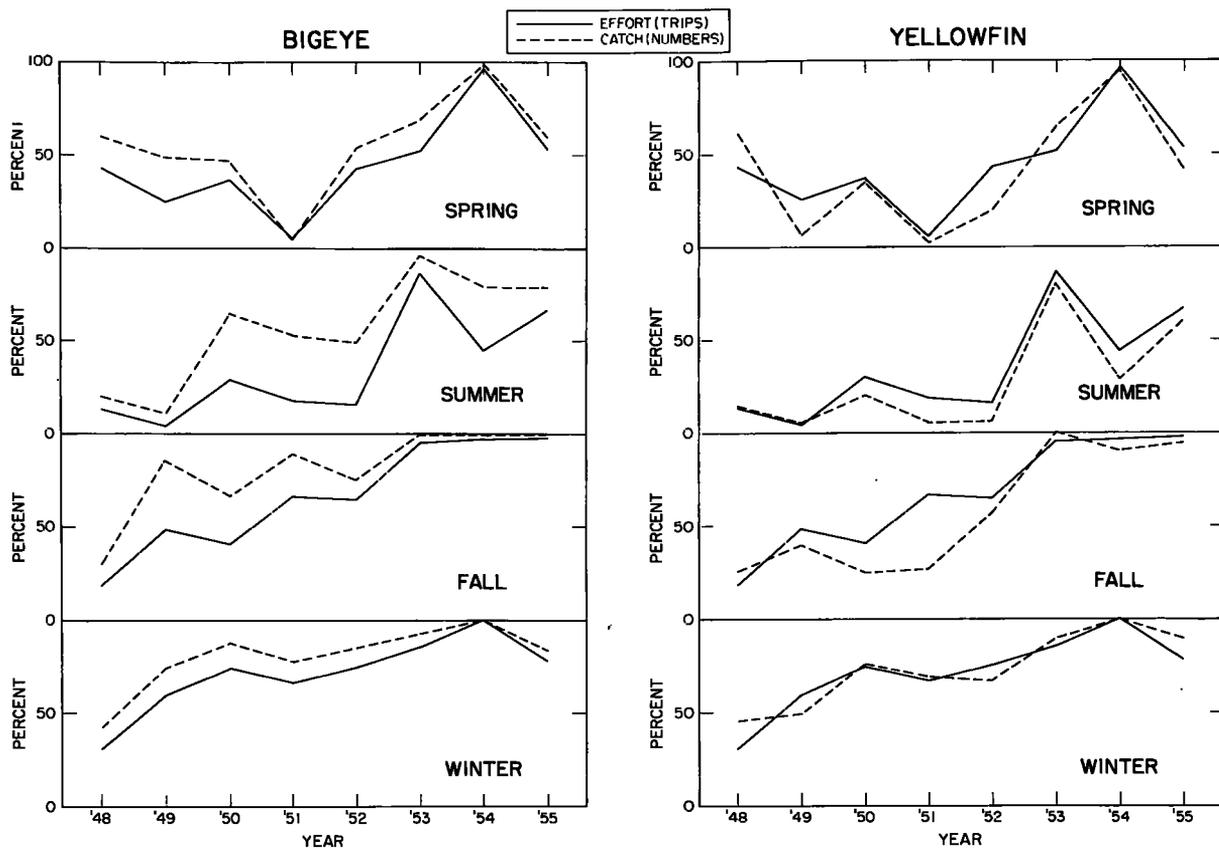


FIGURE 10.—Bigeye and yellowfin catch and fishing effort of large vessels, by seasons, in the windward waters of the southern islands. (See appendix tables 3 and 4.)

the amount of effort expended, whereas the reverse is true of the yellowfin catch. Thus it seems that the differences in availability of the two species in these windward areas are real and not due to a shift in effort among the four seasons.

Firm evidence of areal differences in the availability of the two species is shown by a comparison of the distribution of effort and the resulting catch in the windward area by the small vessels (fig. 11). To reduce the variation due to the seasonal shift in effort, this comparison has been confined to the winter and spring seasons, December through May. Considering the small amount of data available, the possibility of an error in the magnitude of the catches cannot be denied; however, the consistently higher percentage of bigeye taken from the windward areas for the effort expended gives evidence that bigeye were more available in the windward than in the leeward areas. Unfortunately, a similar areal comparison cannot be made for yellowfin, since the small vessels

fished almost exclusively in the leeward waters during the height of the yellowfin season.

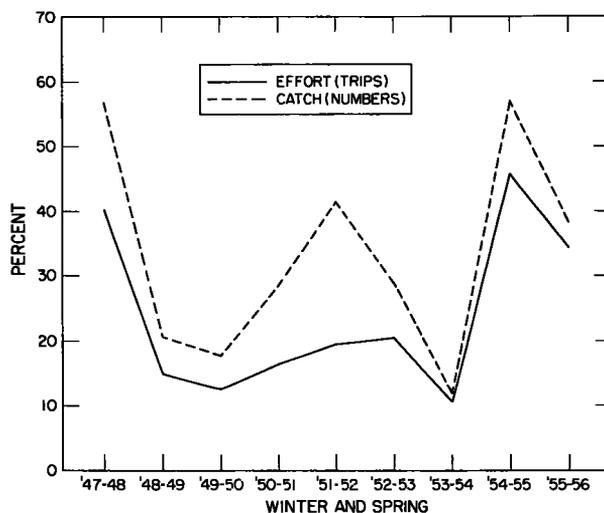


FIGURE 11.—Comparison of fishing effort and bigeye catch in windward areas by small vessels, winter and spring seasons combined. (See appendix table 5.)

In summary, the increase in landings of bigeye and the decline in landings of yellowfin can be related largely to a shift in fishing area by the large vessels from the lee of the northern islands to the windward waters of the southern islands. However, this does not preclude the existence of natural fluctuations in availability, since the catch rates of the small vessels, which did not participate in this shift, show a peak in bigeye during the 1951-52 season. Otsu (1954) points out that on several occasions during this season the catches were limited to prevent flooding of the fresh-fish market. The yellowfin, too, show natural fluctuations, as evidenced by the decline in catch rate of the small vessels during 1955.

SEASONAL DISTRIBUTION OF BIGEYE AND YELLOWFIN

A composite of the monthly average catch rates over the entire period is not the best means of depicting the seasonal distribution of bigeye and yellowfin tuna, but the lack of precise data precludes a detailed examination. This method, however, does show the seasonal trends and for this purpose the data are presented as such in figure 12.

The bigeye season can be considered to occur from October through May, when the large vessels made catches of better than 10 bigeye per trip and the small vessels from 5 to 12 bigeye per trip. The average monthly catches (fig. 7) for the large vessels showed considerable variation, which is

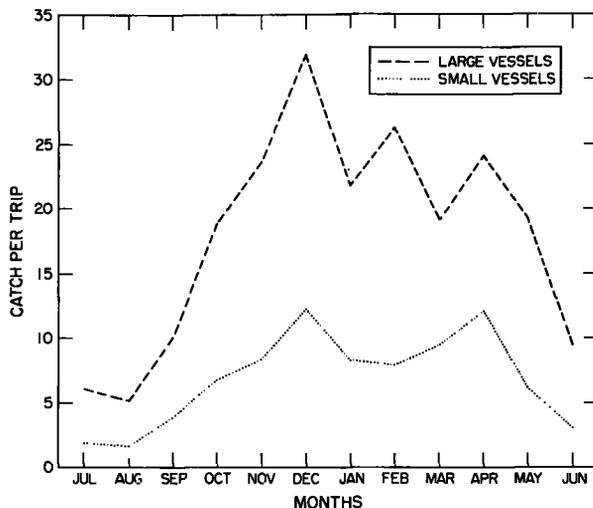


FIGURE 12.—Composite catch per trip of bigeye tuna for small and large vessels, July 1948 to June 1956.

reflected in the composite catch per trip, with peaks during December, February, and April and lows during January and March. On the other hand, the small vessel category shows only one depression covering January through March. This double peaking of the bigeye catches for the small vessels appears to hold true even for individual years; e.g., 1949-50 and 1953-54 (fig. 7). One possibility which could account for the low points would be the inability of the vessels to fish because of bad weather. This would be expected to affect the catch rates inasmuch as the trip is used as the unit of effort. A cursory examination of the days on which small craft warnings were issued by the U. S. Weather Bureau (table 6) shows that there is some correlation of low catches with bad weather. At the present time, however, we are unable to make any quantitative estimates of the effect of weather on catch and fishing effort.

The yellowfin season extends over the summer months and unlike the more gradual entrance of the bigeye into the fishery, the yellowfin enters abruptly during the month of June (fig. 13). This is indicated by the high catch rate of nearly 10 yellowfin per trip for both small and large

TABLE 6.—Number of days with small craft warnings

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
1951-52	2	4	1	3	0	9	1	0
1952-53	0	10	1	0	4	0	0	0
1953-54	1	6	1	3	2	3	1	0
1954-55	1	3	8	1	9	5	6	0
1955	0	9	2					

NOTE.—Unpublished data furnished by U.S. Weather Bureau.

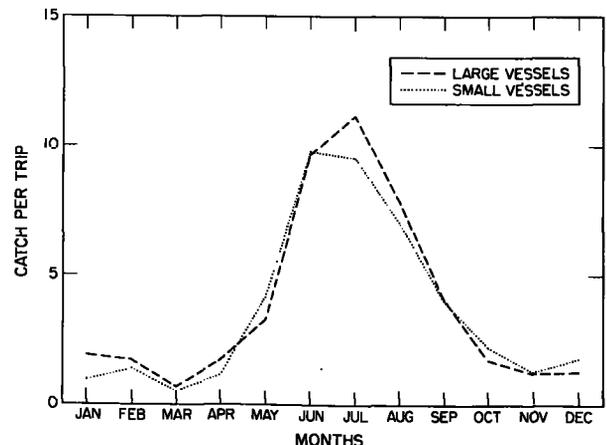


FIGURE 13.—Composite catch per trip of yellowfin tuna for small and large vessels, 1948 to 1956.

vessels during June compared with the low of about 4 fish per trip during the previous month. The rapid decline of the catch rates during August and September, from eight yellowfin per trip to four, also suggests a rather rapid movement of the yellowfin from the fishing grounds.

The yellowfin catch shows uniform single modes for both small and large vessels. This absence of fluctuations could possibly be due to a more uniform number of days fished per trip, a result of the generally good weather which prevails during the summer months. As pointed out in the earlier discussion, there are significant differences in the relative fishing success for bigeye and yellowfin, related to vessel size. The catch rates for yellowfin by small and large vessels were approximately equal throughout the year, whereas for bigeye the large vessels experienced 2.5 times better fishing than the small vessels.

SIZE OF FISH

The Hawaiian longline fishery, by virtue of the method of fishing, primarily exploits the large tunas, a majority of the catch being composed of fish exceeding 100 pounds in weight. The lack of small fish in the catch is not due to their absence from the area, for Moore (1951) has reported that small bigeye and yellowfin are taken in Hawaiian waters by surface-fishing methods; but more likely it is due to a differential size segregation of the species with depth. Bigeye and yellowfin appear to spend their early life near the surface and their adult life in deeper waters, thus the small fish are not available to the deep-fishing longline gear (Murphy and Shomura, 1953).

As noted previously and shown in figure 12, good bigeye catches are made in Hawaiian waters from October through May and only during the summer months are the catches considered poor. In their work on albacore and bigeye (Honma and Kamimura, 1955; Suda 1954), the Japanese have shown that west of the 180° meridian these two species undergo a latitudinal migration, being taken farthest to the north during the summer period and to the south during the winter months. They also present some evidence that at any given time small fish are located to the north of the larger fish, the net result being a gradation in sizes with progressively larger fish to the south. Some evidence of such a phenomenon in the Ha-

waiian fishery is indicated by the changes in average size of the bigeye (fig. 14). Despite the variability of the averages from month to month, the catch was composed of consistently smaller fish during the winter months, as is to be expected if the larger fish in a population sorted by size did move to the south during the winter.

Another interesting size variability in the catch is the consistently lower average size of bigeye taken by the small vessels as compared with those taken by the large vessels. This difference, which is most noticeable during the winter months (fig. 14), is clearly indicated in a comparison of the annual average size of bigeye by size of vessel (fig. 15). Although the magnitude of the differences is not important, the consistency of the relation, i.e., small fish being captured by small vessels, is striking. This may be confirming evidence of the size gradation with latitude, inasmuch as the small vessels operate in waters farther north than the large vessels.

The yellowfin also show considerable seasonal fluctuations in average size, with the larger fish occurring during the summer months when the catches are best (fig. 14). Unlike the bigeye, there are no pronounced differences in the annual average size of yellowfin taken by small and large vessels (fig. 15).

DISCUSSION

At present, little is known of the life histories of the various tuna species. Research has been conducted on various segments of the biology of the bigeye and yellowfin in Hawaiian waters (Brock 1949, June 1953, Otsu 1954, Iversen 1956, and Yuen 1955). Utilizing all available information, we have constructed a hypothesis to explain the presence of the bigeye in Hawaiian waters. In brief, this assumes that bigeye tuna spawn in tropical waters south of the Hawaiian Islands and that the young fish migrate to the north of Hawaii. Superimposed on this migration of the young fish are regular, seasonal north-south migrations of the adult population.

This explanation is based on the following information. Yuen (1955) established that the bigeye in Hawaiian waters are not in spawning condition, and thus their presence in the longline fishery cannot be attributed to a spawning run, such as was suggested for the yellowfin by June

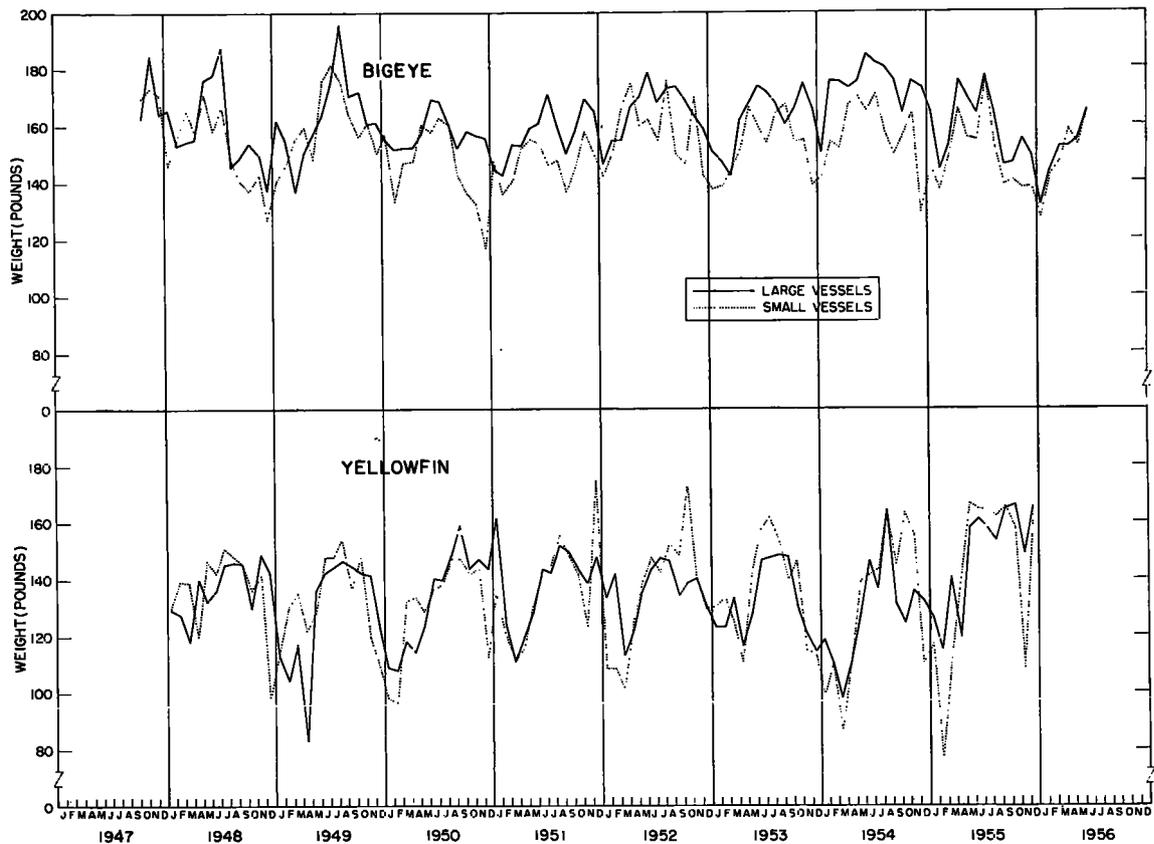


FIGURE 14.—Average size of bigeye and yellowfin, by months, in the catch of small and large vessels.

(1953). Maturation studies show that bigeye spawn more than once a year and that they have a widespread spawning area extending from the waters southeast of the Hawaiian Islands and westward to the Caroline Islands group (Yuen 1955). The presence of small bigeye in Hawaiian waters has been demonstrated (Moore 1951), but no studies have been made on the details of their distribution or seasonal variability.

According to our hypothesis, the adult bigeye population shifts southward during the winter, bringing the fish within reach of the Hawaiian fishery. Since the fish remain segregated by size, an auxiliary effect of this southern migration is to reduce the size of the fish taken in Hawaii in winter as compared with the size taken during the summer. Even during the winter it appears that the peak density of the population lies to the north of Hawaii, for Japanese vessels, specifically searching for bigeye, fish from 100 to 200 miles north of the Hawaiian Islands chain during Janu-

ary and February. Following the winter, the northward shift of the population leaves the Hawaiian Islands on the extreme southern fringe of the distribution and the catch rates of bigeye drop precipitously, though a few relatively large individuals are taken. It is during this period of low bigeye catch that the large yellowfin move into the Hawaiian Islands area.

SUMMARY

1. A detailed examination of the catch records of the Honolulu longline fleet, covering the period 1948 to 1956, was made to determine the causes of a marked increase in landings of bigeye tuna and a decline in yellowfin.

2. A study of the fishing effort expended in the fishery showed a substantial increase in the total number of trips, resulting from an increase in the number of trips per vessel and from the addition of new vessels to the fleet. The magnitude of the increase in effort was not sufficient, however, to

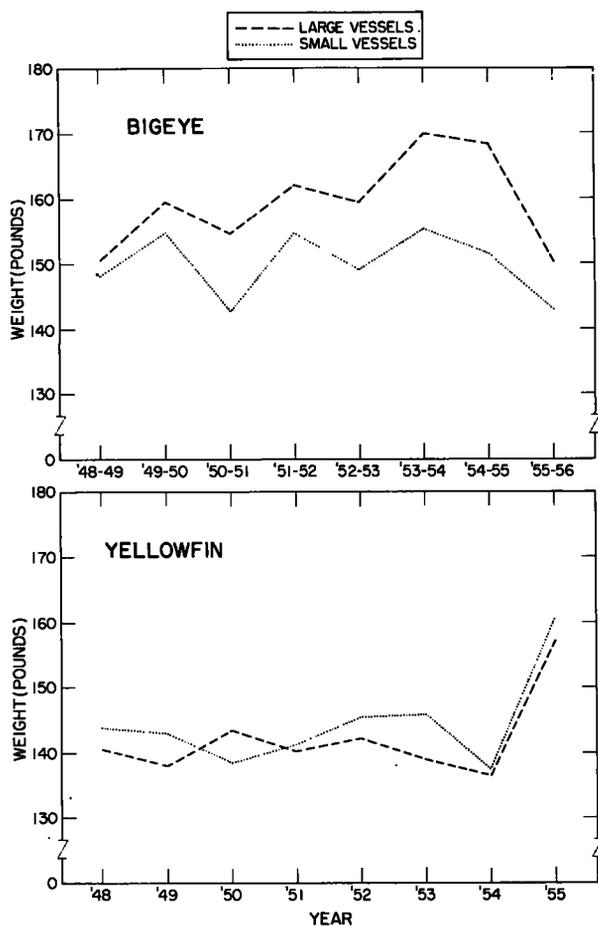


FIGURE 15.—Average annual size of bigeye (by fiscal year) and yellowfin (by calendar year) taken by small and large vessels.

account for all of the increase in bigeye landings and did not explain the decline in yellowfin.

3. When the catch-per-trip data were classified according to size of vessel, they showed a generally stable catch rate for both bigeye and yellowfin by the small vessels during the period under study but an increase in catch per trip for the bigeye by the large vessels, accompanied by a decline in yellowfin during the last 3 years (1953–55). This divergence was explained on the basis of a shift in area of fishing by the large vessels. The small vessels, which concentrated their efforts in waters surrounding Oahu, experienced uniform bigeye and yellowfin catches. The large vessels, on the other hand, shifted from the leeward areas of the northern islands to the windward areas of the southern islands. The increase in bigeye catch rate was due to the greater availability of bigeye

in the windward areas as compared with the leeward areas. The decline in yellowfin catch rates by the large vessels during the last 3 years of this study was related to the increased fishing effort during the summer in the windward areas of the southern islands, which are areas of reduced yellowfin availability.

4. Annual variations in availability not due to areal shifts in the fishery were shown in the catch rates of the small vessels. The 1951–52 season was exceptionally good for bigeye, while the yellowfin showed a decline in availability during the 1955 season.

5. The bigeye captured by the small vessels were consistently smaller than those captured by the large vessels, and the smallest bigeye were taken during the winter months.

6. A hypothesis explaining the seasonal variability in bigeye distribution has been developed utilizing the results from various studies on the life history of the bigeye and on the commercial fishery. Essentially, it assumes that spawning takes place in tropical waters followed by a migration of the small fish northward to a center of abundance located north of the Hawaiian Islands. The adult population undertakes a north-south seasonal migration, spending the winter and spring months in Hawaiian waters, where it supports a sizable longline fishery.

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APPENDIX

APPENDIX TABLE 1.—Annual landings (pounds) of bigeye and yellowfin tuna, 1946 to 1956

Year	Total Hawaiian landings (all types of gear)	Total longline landings	Total landings Honolulu-based longline fleet	Year	Total Hawaiian landings (all types of gear)	Total longline landings	Total landings Honolulu-based longline fleet
Bigeye:				Yellowfin:			
1946-47	199,007			1946	1,324,767		
1947-48	621,794			1947	1,314,349		
1948-49	632,269	630,935	460,705	1948	1,158,111	1,006,460	365,717
1949-50	1,707,884	1,706,035	1,138,454	1949	929,239	817,057	307,201
1950-51	1,820,584	1,819,008	1,215,505	1950	720,537	605,315	363,916
1951-52	2,252,985	2,248,640	1,721,017	1951	757,199	661,314	368,686
1952-53	2,496,162	2,473,533	1,648,006	1952	855,655	719,329	454,819
1953-54	2,710,437	2,698,890	2,032,208	1953	621,654	459,196	272,214
1954-55	2,346,682	2,340,824	1,680,600	1954	525,770	435,551	322,237
1955-56	2,241,782	2,231,468	1,526,922	1955	445,709	352,781	229,191

APPENDIX TABLE 2.—Catch of bigeye and yellowfin and fishing effort of large vessels in windward waters of the southern islands, 1948 to 1956

I. BIGEYE (FISCAL YEAR)

	1948-49	1949-50	1950-51	1951-52	1952-53	1953-54	1954-55	1955-56
Windward waters of southern islands:								
Effort (trips)	82	131	110	149	133	133	101	106
Catch (number)	740	3,053	2,919	4,922	3,540	4,170	3,179	2,786
All areas:								
Effort (trips)	282	319	319	314	241	157	135	150
Catch (number)	1,823	4,528	5,360	6,999	4,595	4,332	3,539	3,529

II. YELLOWFIN (CALENDAR YEAR)

	1948	1949	1950	1951	1952	1953	1954	1955
Windward waters of southern islands:								
Effort (trips)	76	99	138	129	150	129	110	112
Catch (number)	367	191	335	188	325	283	260	161
All areas:								
Effort (trips)	280	298	340	298	328	161	134	144
Catch (number)	1,400	1,260	1,383	1,267	1,810	351	468	243

APPENDIX TABLE 3.—Bigeye catch and fishing effort by seasons, of large vessels, 1948 to 1955

	1948	1949	1950	1951	1952	1953	1954	1955
Spring:								
Windward waters of southern islands:								
Effort (trips)	30	18	32	5	35	22	34	18
Catch (number)	328	337	695	76	1,190	806	1,166	379
All areas:								
Effort (trips)	70	68	86	81	81	42	35	34
Catch (number)	545	693	1,437	1,670	2,198	1,164	1,181	643
Summer:								
Windward waters of southern islands:								
Effort (trips)	9	3	24	12	14	34	14	24
Catch (number)	30	19	417	311	243	555	216	288
All areas:								
Effort (trips)	69	71	84	67	89	39	32	36
Catch (number)	149	172	638	591	496	373	273	365
Fall:								
Windward waters of southern islands:								
Effort (trips)	14	39	34	57	50	41	33	39
Catch (number)	101	735	838	1,541	1,001	1,251	1,249	1,048
All areas:								
Effort (trips)	77	82	83	85	77	43	34	40
Catch (number)	347	856	1,247	1,726	1,322	1,264	1,258	1,052
Winter:								
Windward waters of southern islands:								
Effort (trips)	21	44	56	48	40	36	32	29
Catch (number)	260	1,355	1,643	1,993	1,380	1,329	1,339	1,007
All areas:								
Effort (trips)	68	75	76	72	53	42	32	37
Catch (number)	611	1,824	1,859	2,564	1,602	1,423	1,339	1,196

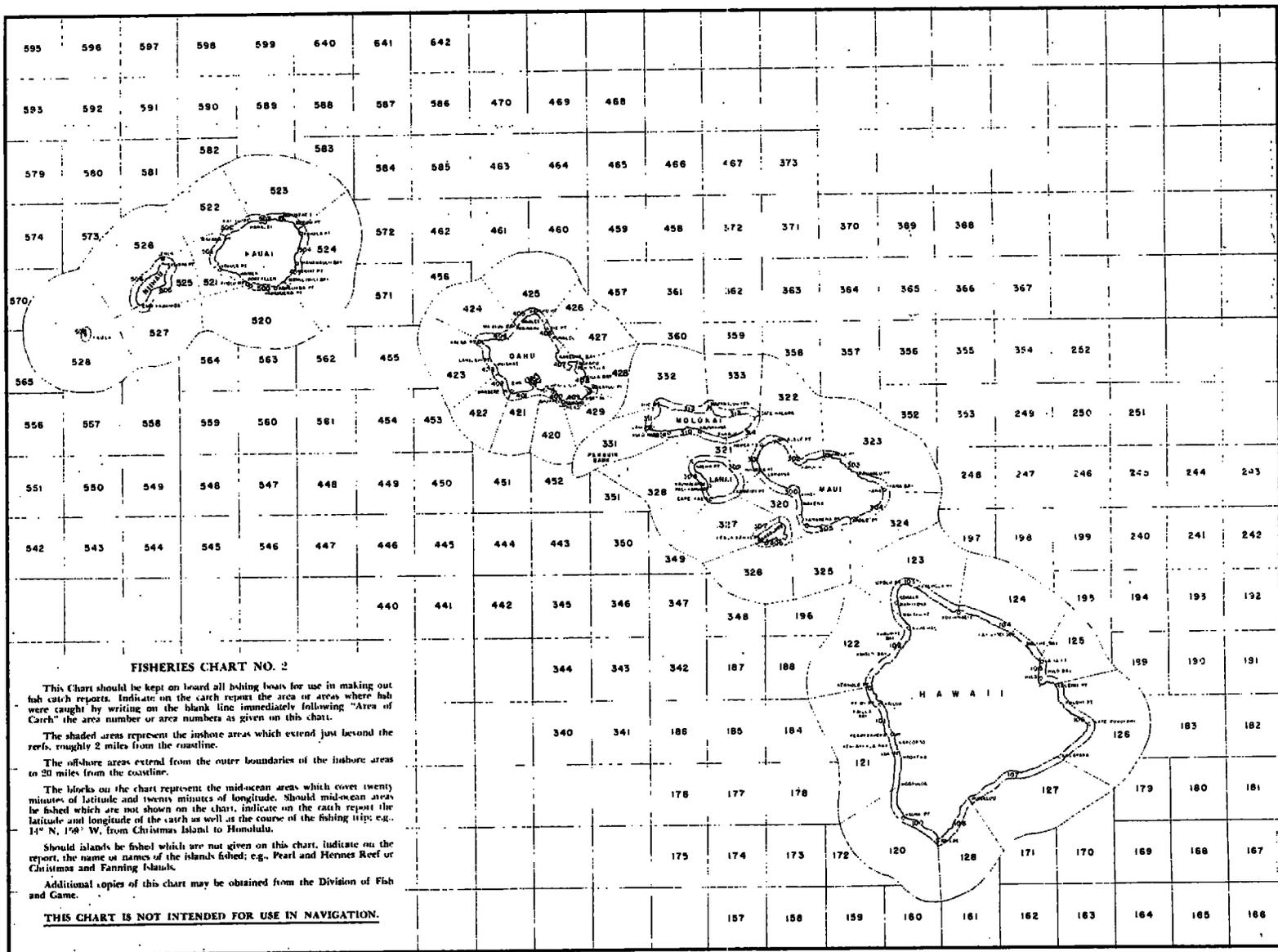
APPENDIX TABLE 4.—*Yellowfin catch and fishing effort, by seasons, of large vessels, 1948 to 1955*

	1948	1949	1950	1951	1952	1953	1954	1955
Spring:				1				
Windward waters of southern islands:								
Effort (trips).....	30	18	32	5	35	22	34	18
Catch (number).....	100	10	28	6	45	22	50	8
All areas:								
Effort (trips).....	70	68	86	81	81	42	35	34
Catch (number).....	162	153	82	339	221	34	53	19
Summer:								
Windward waters of southern islands:								
Effort (trips).....	9	3	24	12	14	34	14	24
Catch (number).....	111	40	177	33	81	158	75	101
All areas:								
Effort (trips).....	69	71	84	67	89	39	32	36
Catch (number).....	784	803	881	608	1,260	198	269	168
Fall:								
Windward waters of southern islands:								
Effort (trips).....	14	39	34	57	50	41	33	39
Catch (number).....	90	71	76	62	100	46	61	32
All areas:								
Effort (trips).....	77	82	83	85	77	43	34	40
Catch (number).....	341	181	307	233	176	46	67	34
Winter:								
Windward waters of southern islands:								
Effort (trips).....	21	44	56	48	40	36	32	29
Catch (number).....	61	33	117	57	78	100	24	26
All areas:								
Effort (trips).....	68	75	76	72	53	42	32	37
Catch (number).....	134	67	153	83	116	111	24	29

APPENDIX TABLE 5.—*Bigeye catch and effort by small vessels in all windward areas, 1947 to 1956*

[Winter and spring seasons combined]

	1947-48	1948-49	1949-50	1950-51	1951-52	1952-53	1953-54	1954-55	1955-56
Windward areas:									
Effort (trips).....	29	13	13	19	9	15	5	22	12
Catch (number).....	231	83	191	279	272	221	63	255	260
All areas:									
Effort (trips).....	72	87	105	116	46	73	47	48	35
Catch (number).....	407	405	1,077	977	656	766	535	447	678



APPENDIX FIGURE 2.—Hawaiian Division of Fish and Game fisheries chart No. 2, showing the statistical areas.

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

VERTICAL DISTRIBUTION OF PELAGIC FISH EGGS AND LARVAE OFF CALIFORNIA AND BAJA CALIFORNIA

By ELBERT H. AHLSTROM



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ABSTRACT

Information is given on the vertical distribution of 46 kinds of fish larvae and 8 kinds of fish eggs, as determined from 22 series of hauls made at 15 stations off southern California and central Baja California. Each series consisted of 6 to 11 hauls taken with a closing net at successively deeper levels.

Most fish eggs and larvae were found to occur in the upper mixed layer and in the upper part of the thermocline between the surface and approximately 125 meters deep. All of the more common kinds of larvae showed marked differences in vertical distribution from series to series.

Replicate vertical distribution series were taken at seven stations, one in daylight, the other during darkness. Larvae of sardine, anchovy, and *Leuroglossus stilbius* were four to five times as abundant in night series as in day. The night-to-day ratio for all larvae was 2 to 3.

Supplementary information on vertical distribution of larvae was obtained on Norpac, where two levels (131-0 meters and 262-131 meters) were fished at most stations.

VERTICAL DISTRIBUTION OF PELAGIC FISH EGGS AND LARVAE OFF CALIFORNIA AND BAJA CALIFORNIA

By **ELBERT H. AHLSTROM**, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

A prerequisite to any program of quantitative sampling of plankton organisms, such as the pelagic eggs and larvae of fishes, is a knowledge of their depth distributions. We have been interested primarily in quantitative sampling of sardine eggs and larvae, and a number of studies have been made to determine their vertical distributions (Silliman 1943, Ahlstrom 1948, Ahlstrom et al. 1958). Simultaneously, information has been obtained on the vertical distributions of various other fish eggs and larvae. For some species the information is limited to one or a few observations, for others it is complete enough to fairly well delimit their vertical ranges.

METHODS AND MATERIALS

Twenty-two series of hauls were made at 15 stations to study the vertical distribution of fish

eggs and larvae (fig. 1). Each series consisted of 6 to 11 hauls taken with a closing net at successively deeper levels. In the nine series made in 1941, each haul covered a limited depth stratum, such as 0-4 meters, 10-15 meters, and 25-30 meters. In the 13 series made in 1952 through 1955, horizontal hauls were taken at a number of depths. Despite these minor differences in obtaining hauls, the series taken during the two periods are roughly comparable. A record of haul data for the 206 hauls that comprise the 22 vertical series is contained in the appendix and the average depths of hauls are summarized in table 1.

Replicate series were made at seven stations, one during the night, the other during daylight, in order to study diurnal changes in vertical

NOTE.—Approved for publication, July 28, 1958. *Fishery Bulletin* 161.

TABLE 1.—Average depths of hauls in 22 series of closing-net tows made to study vertical distribution of fish eggs and larvae

Station series	Average depth (m.) of haul No. —										
	1	2	3	4	5	6	7	8	9	10	11
4104-91.54	3	8	18	24	37	54	72				
4105-89.38	3	8	18	25	36	56	73				
4105-92.39	3	10	20	28	40	58	76	112			
4106-94.37N	3	9	20	27	41	58	69	100			
4106-94.37D	3	9	19	30	41	58	73	105	139		
4106-94.47N	3	10	21	27	44	59	76	107	141		
4106-94.47D	3	9	21	28	42	60	76	110	141		
4106-97.43N	3	10	21	27	43	57	79	106	142		
4106-97.43D	3	10	20	28	42	60	77	104	133		
5206-90.28N	2	7	17	27	42	57	73	107	142	206	286
5206-90.28D	2	7	18	29	44	56	71	105	134	216	286
5208-120.35	3	10	18	27	36	51					
5303-91.38N	2	7	18	29	41	54	66	106	150	211	291
5303-91.38D	2	7	18	28	42	56	72	92	139	206	
5305-93.50N	2	6	21	29	43	57	70	106	138	222	276
5305-93.50D	2	7	16	25	33	46	63	103	138	239	
5403-94.80N	2	7	17	27	42	52	64	101	127	200	
5403-94.80D	2	7	18	28	41	53	68	102	135	201	
5504-107.80	2	8	20	31	45	57	*70	111	142		
5504-110.60	2	7	18	29	44	58	*73	105			
5504-120.50	2	7	18	27	44	60	*74	110	137	225	
5504-130.60	2	8	17	28	42	56	*72	102	136	215	
Average	2	8	19	28	41	56	72	105	138	215	285
Standard deviation	0.5	1.3	1.5	1.6	3.1	3.4	4.0	4.6	5.1	12.1	
Meters of depth represented by haul	5	8	10	11	14	16	24	33	55	73	70

*Hauls taken at approximately 88 meters depth on cruise 5504 are omitted from this tabulation.

distribution and abundance of larvae. Night series at these stations are designated with an "N," day series with a "D." The differences between night and day series will be discussed in a latter section of the paper.

Coverage was most intensive in the upper 100-meter stratum: Five hauls were taken above 50 meters with average depths of 2, 8, 19, 28, and 41 meters; two hauls were made between 50 and 100 meters with average depths of 56 and 72 meters.

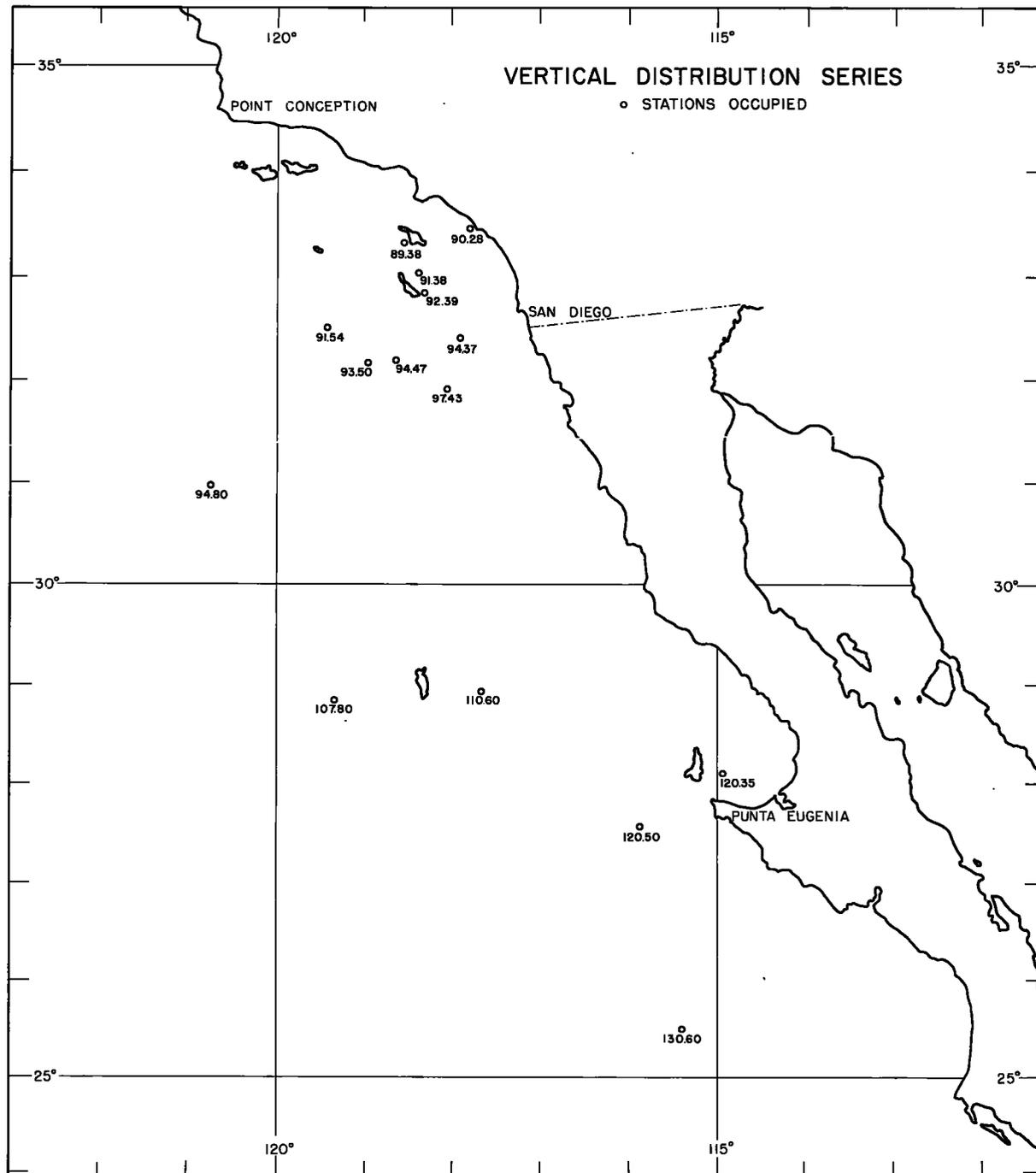


FIGURE 1.—Location of stations at which vertical distribution series were made.

From two to four hauls were usually made below 100 meters with average depths of 105, 138, 215, and 285 meters.

Each of the hauls in a series is assumed to be representative of the distribution within a depth zone. Since the spacing of hauls in depth was not uniform, the widths of zones are narrower for hauls taken near the surface and become progressively greater for deeper hauls.

All hauls were made with closing nets and gear patterned after that described by Leavitt (1935, 1938). Two sizes of closing nets were employed, one measuring 0.5 meter in diameter at the mouth, the other 1.0 meter in diameter at the mouth. A 0.5-meter net was used in 1941 at stations 4104-91.54 and 4105-89.38. It was constructed of No. 40xxx grit gauze with mesh openings of approximately 0.45 millimeter when new, shrinking to approximately 0.30 millimeter after use. The 1.0-meter closing net used in 1941 (series 4105-92.39, 4106-94.37N and D, 4106-94.47 N and D, and 4106-97.43N and D) was constructed of cotton scrim, with mesh openings ranging in width from 0.8 to 1.0 millimeter. The 1.0-meter nets used in taking all subsequent series were constructed of No. 30xxx grit gauze, with mesh openings of approximately 0.55 millimeter width after shrinkage.

All series are numbered according to present usage. The series made in 1941 have been reported in literature under different station numbers (Silliman 1943). To avoid confusion, the equivalents are given below:

Station No. (present usage)	Equivalent in 1941 system	Position		Date of occupancy
		N. latitude	W. longitude	
4104-91.54	2046	32°29'	119°26'	IV-30-41
4105-92.39	2043	32°50'	118°18'	V-2-41
4106-94.37N	2452N	32°23'	117°52'	VI-17, 18-41
4106-94.37D	2452D	32°17'	117°52'	VI-19-41
4106-94.47N	2454N	32°12'	118°38'	VI-18, 19-41
4106-94.47D	2454D	32°10'	118°39'	VI-19-41

We have tried to collect successive hauls of a given series in a comparable manner as regards length of haul and speed of hauling. No attempt has been made, however, to make the several series entirely comparable. Because of the uncertainty of performance of current meters when used with closing nets, they were not employed. Consequently, it has not been possible to determine the volume of water strained in taking hauls. The

series taken during 1941 averaged 15 to 18 minutes per haul; those taken subsequently averaged 10 minutes, occasionally 5 minutes per haul. At station 5305-93.50, towing time was reduced to 5 minutes per haul for a number of the hauls because of the large quantity of plankton material being collected. To adjust for this, counts of larvae for 5-minute hauls were doubled, hence numbers reported for 5305-93.50N and D are comparable for all depths.

In the four series made off central Baja California in 1955, a haul was taken at approximately 88 meters deep (125 meters of wire out)—a level not sampled in previous series. This level was added in order to obtain additional information on distribution of larvae within the thermocline, which was quite deep at these stations. The larvae taken at this level are included in table 2 and in depth-distribution tables for individual species. Inasmuch as this depth was not occupied in taking other series, the data have not been used in obtaining average depth distribution values for most species. Several species occurred almost exclusively in the series made on cruise 5504, especially *Vinciguerria lucetia* and *Diogenichthys laternatus*, and in these instances this level was used.

Vertical distribution series were usually made at localities where eggs and larvae were fairly abundant. Often a large area was scouted before such a rich spot was located. More than 40 localities were sampled on cruise 5504, for example, in order to locate the 4 sites at which vertical series were taken.

The least number of larvae taken in any of the 22 vertical series was 23 in 4106-97.43D, the most was 5,862 in 5504-120.50. Less than 100 larvae were taken in 3 series, between 101 and 500 larvae were obtained in 10 series, between 501 and 1,000 larvae in 3 series, and over 1,000 larvae in 6 series. The combined total for the 22 series was 18,045 larvae.

At least 60 kinds of fish larvae were taken in the vertical series. A summary tabulation of the abundance of 46 kinds of larvae in the 22 series is given in table 2. All other kinds of fish larvae are placed in a category labeled "others." Included as others are gobies, paralepedids, cottids, trichiurids, sciaenids, most blennies, zoarcids, and eel leptocephalids—most of which were identified only to family—and a few larvae that could not

TABLE 2.—Abundance of fish larvae in vertical distribution series taken off California and Baja California, by station

	4104-01.54	4105-89.38	4105-92.39	4105-94.37N	4105-94.37D	4105-94.47N	4105-94.47D	4105-97.43N	4105-97.43D	5205-90.28N	5205-90.28D	5205-120.35	5205-91.38N	5205-91.38D	5205-93.50N	5205-93.50D	5403-94.80N	5403-94.80D	5504-107.80	5504-110.60	5504-120.50	5504-120.60	Total
<i>Sardinops caerulea</i>	734	34	676	40	6	89	24	1	0	5	3	114	0	0	0	0	10	4	35	59	7	1	1,842
<i>Engraulis mordax</i>	342	189	577	27	4	217	10	12	0	612	151	125	12	0	10	20	0	0	543	15	5,144	1	7,991
<i>Trachurus symmetricus</i>	4	0	21	0	1	7	0	0	0	26	2	0	0	0	4	2	52	210	72	297	86	0	784
<i>Pleuronichthys diego</i>	0	0	62	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	147	0	217
<i>Merluccius productus</i>	36	21	22	3	0	8	0	1	0	0	0	20	0	0	0	0	1,753	707	214	2	100	0	2,892
<i>Sebastes</i> spp.....	97	39	67	20	46	41	65	0	1	48	33	0	225	45	124	144	0	0	15	40	216	0	1,267
<i>Citharichthys</i> spp.....	7	2	8	0	2	3	3	1	0	1	0	102	17	0	4	4	0	0	0	0	21	0	181
<i>Lyopsetta erilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	10
<i>Paralichthys californicus</i>	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
<i>Pleuronichthys decurrens</i>	0	0	0	0	0	0	0	0	0	0	0	4	4	0	0	0	0	0	0	0	0	0	8
<i>Symphurus atricauda</i>	0	0	0	0	0	0	0	0	0	0	0	39	0	0	0	0	0	0	0	0	0	0	39
<i>Lampanyctus leucopsarus</i>	35	18	25	0	4	6	7	1	0	158	4	0	119	60	51	112	10	9	0	0	0	0	619
<i>Lampanyctus mexicanus</i>	0	1	15	5	1	19	2	27	14	3	0	0	0	0	2	0	0	0	88	36	22	33	273
<i>Lampanyctus ritleri</i>	5	2	19	1	2	1	0	4	6	1	2	0	9	5	10	4	19	21	38	11	13	0	173
<i>Tarletonbeania crenularis</i>	0	0	0	0	0	0	0	0	0	13	34	0	1	1	11	6	0	0	0	0	0	0	66
<i>Diogenichthys laternatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	1	0	108
<i>Diogenichthys atlanticus</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	5
<i>Electrona</i> spp.....	1	0	0	2	0	5	0	0	0	1	0	0	1	0	0	0	4	1	3	0	2	0	20
<i>Lampanyctus regalis</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Loveina rara</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Myctophum californiense</i>	0	0	2	0	1	2	0	2	0	0	0	0	0	0	0	0	1	0	9	0	1	0	18
<i>Myctophum margaritatum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Leuroglossus stilbius</i>	18	0	70	2	1	22	1	1	0	60	30	0	480	74	25	7	2	5	66	4	61	0	838
<i>Bathylagus wesethi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	6	0	84
<i>Argentina sialis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3	0	4
<i>Bathylagus alascanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Bathylagus</i> sp.....	5	0	14	2	1	6	2	1	0	3	0	0	8	1	0	2	0	0	1	0	1	0	47
<i>Microstoma</i> sp.....	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	3	0	0	0	0	0	5
<i>Nansenia</i> sp.....	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
<i>Vinciguerria lucetia</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	16	25	5	112	0	0	150
<i>Argyropelecus</i> spp.....	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	2	6
<i>Aristostomias scintillans</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Chauliodus macouni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	2
<i>Cyclothone</i> spp.....	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	7	3	11	30
<i>Ichthyococcus</i> sp.....	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Idiacanthus antrostomus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
<i>Stomias atriporter</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
<i>Brosomphycis marginata</i>	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	3
<i>Chromis punctipinnis</i>	0	0	0	0	0	0	5	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0	11
<i>Colobis saira</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	3
<i>Ichthyus lockingtoni</i>	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	5
<i>Melamphaes</i> spp.....	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3	6	2	0	0	0	14
<i>Palometa similima</i>	0	3	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	5	0	13
<i>Sphyraena argentea</i>	0	3	0	0	0	0	0	0	0	4	10	0	0	0	0	0	0	0	0	0	0	0	17
<i>Trachipterus versalmonorum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2
Labrids.....	0	4	8	0	0	2	11	0	0	57	1	0	1	0	0	4	0	0	0	0	1	0	80
Others.....	3	1	5	1	0	5	1	0	0	23	7	38	50	6	3	14	4	0	7	0	6	5	179
Total.....	1,288	297	1,592	103	70	444	132	53	23	1,023	281	424	925	208	245	323	1,875	966	1,124	502	5,862	282	18,045

be identified with certainty. A total of 179 larvae are included in this category, slightly less than 1 percent of the total.

It is interesting to note that despite the fact that most vertical series were taken off southern California in areas where sardine spawning might be taking place, the series do reflect fairly well the abundance of fish larvae in the California Cooperative Oceanic Fisheries Investigations (CCOFI) survey area. The relative abundance of the 15 most common kinds of larvae taken in vertical series is compared with their relative abundance in the CCOFI area during 1955 and 1956 in table 3. Fourteen of these ranked among the 15 most common kinds of larvae taken during the 1955 survey cruises, and 12 ranked among the 15 most common kinds of larvae taken in 1956.

Anchovy larvae ranked first in abundance, hake larvae second in the three tabulations. The con-

scious selection for sardine larvae when taking vertical series raised them to third place in abundance in the vertical series, but sardine larvae ranked sixth in abundance in yearly totals for both 1955 and 1956. For the same reason, jack mackerel and Pacific mackerel have a somewhat higher rank in vertical series than in yearly totals. The relative abundance of *Sebastes* spp., *Leuroglossus stilbius*, *Lampanyctus leucopsarus*, and *Lampanyctus mexicanus* are strikingly similar in all three tabulations.

Detailed information on depth distribution is given for 46 kinds of larvae taken in vertical distribution series. The data for each of the 15 most common kinds of larvae are summarized in individual tables (tables 5-11, 14-18, 20, 21, 23); the data for the remaining 31 categories are summarized in 4 tables, as follows: 4 kinds of other flatfish (table 12), 6 kinds of other myctophids

TABLE 3.—Comparison of relative abundance of fish larvae in vertical distribution series with their abundance in survey cruises of the California Cooperative Oceanic Fisheries Investigations in 1955 and 1956

Species	Fish larvae taken in vertical series			Total fish larvae taken in 1955			Total fish larvae taken in 1956		
	Number taken	Percent of total	Rank	Number taken ¹	Percent of total	Rank	Number taken ¹	Percent of total	Rank
<i>Engraulis mordax</i>	7,991	44.28	1	140,183	39.03	1	134,931	33.06	1
<i>Merluccius productus</i>	2,892	16.03	2	60,090	16.73	2	94,277	23.10	2
<i>Sardinops caerulea</i>	1,842	10.21	3	14,121	3.93	6	15,523	3.80	6
<i>Sebastes</i> spp.....	1,267	7.02	4	29,344	8.17	3	29,144	7.14	3
<i>Leuroglossus stilbius</i>	838	4.64	5	15,111	4.21	5	18,620	4.56	5
<i>Trachurus symmetricus</i>	784	4.34	6	13,246	3.69	7	8,027	1.97	10
<i>Lampanyctus leucopaeus</i>	619	3.43	7	7,454	2.08	10	15,125	3.71	7
<i>Lampanyctus mexicanus</i>	273	1.51	8	13,165	3.67	8	10,802	2.65	8
<i>Pneumatophorus diego</i>	217	1.20	9	1,950	.54	14	1,520	.37	20
<i>Citharichthys</i> spp.....	181	1.00	10	20,411	5.68	4	23,635	5.79	4
<i>Lampanyctus ritleri</i>	173	.96	11	1,988	.55	13	1,924	.47	18
<i>Vinciguerrilla lucella</i>	159	.88	12	12,654	3.52	9	9,832	2.41	9
<i>Diogenichthys lateralis</i>	110	.61	13	4,771	1.33	11	3,158	.77	13
<i>Bathylagus wesethi</i>	84	.47	14	3,245	.90	12	2,146	.53	17
<i>Tarletonbeania crenularis</i>	66	.37	15	999	.28	22	3,352	.82	12
All others.....	549	3.04	-----	20,423	5.69	-----	36,124	8.85	-----
Total.....	18,045	99.99	-----	359,155	100.00	-----	408,140	100.00	-----

¹ Standard haul totals.

(table 19), 5 kinds of other deep-sea smelts (table 22), and 16 kinds of other fish larvae (table 24). Of the 46 kinds of larvae dealt with in the tables, 38 represent individual species, 7 represent genera, and 1 grouping is by family (Labridae).

Illustrations of depth distributions are of two kinds: those based on the average distribution of a category in all the series in which it occurs (figs. 2, 3, and 12), and those based on the distribution of eggs or larvae of a species (or genus) at individual stations (figs. 4-11, 13). In the latter a temperature profile is superimposed over each depth diagram.

Average vertical distributions, illustrated in figures 2, 3, and 12, are not based on a summation of the numbers taken in individual series. If this were done, undue weight would be given to a series in which a category was unusually abundant—such as series 5504-120.50 for *Engraulis mordax*, or series 5403-94.80N for *Merluccius productus*. Instead, equal weight has been given to each series in which a category was common to abundant (50 or more larvae per series) by changing numbers into percentages; thus, each of the larger series has an equal weight of 100. All series in which a category was rare to rather common (1 to 49) were combined and the composite was given a weight of 100. As an example, *Trachurus symmetricus* larvae occurred in 13 series. In 5 series more than 50 larvae were taken per series, and each of these was weighted to 100. The composite of the other 8 series (which totaled only 67 individuals) was given a group weight of 100. The 6 weighted series (5 individual and 1 com-

posite) were then combined and used to determine the percentage occurrence at each level. Illustrations of depth distributions at individual stations also are based on percentage occurrence at each level rather than on actual number (figs. 4-11 and 13).

Depth distributions of eggs are given for 8 of the 15 common kinds of fishes. Of the other seven common categories, *Sebastes* is ovoviviparous, the eggs of myctophids are unknown, and *Citharichthys* eggs were uncommon. Sardine and anchovy eggs were identified from all collections; the eggs of other fishes were identified from only eight series (5303-91.38N and D, 5403-94.80N and D, and the four series taken on cruise 5504).

Less complete data on the vertical distribution of eggs and larvae are available from two other sources. High-speed samplers have been towed simultaneously at four depths during special studies made with these instruments, usually at approximately 10, 20, 30, and 40 meters deep. The results are presented in a separate report (Ahlgren et al. 1958). These samplers have been shown to be exceedingly useful instruments in studying variations in the depth distribution of eggs and larvae within the upper 40-meter level. They are of less use in studying the complete depth ranges of eggs and larvae since present models can be hauled only at shallow depths (to perhaps 50 meters), hence cannot be used for encompassing the depth distributions of most fish eggs and larvae.

On some regular survey cruises a 1.0-meter closing net has been used to sample a depth zone below that sampled in taking the standard 1.0-meter net haul. This procedure was followed during the 1939 and 1940 cruises, for example, and the information thus obtained on the depth distribution of sardine eggs and larvae was summarized by Ahlstrom (1948). Two hauls were taken simultaneously at most stations during Norpac, the upper standard net haul sampling a depth zone from approximately 131 meters deep to the surface, the closing net sampling the level between approximately 262 and 131 meters deep. A brief comparison of the kinds and numbers of larvae taken in the two levels during Norpac is given in a latter section of this report.

The vertical distribution series were taken from five research vessels: *E. W. Scripps*, *Crest*, *Horizon*, and *Spencer F. Baird*, operated by the Scripps Institution of Oceanography, and the *Black Douglas*, operated by the U.S. Fish and Wildlife Service. Personnel of the Scripps Institution of Oceanography cooperated in the collection of material at sea. Many persons presently or formerly employed by the La Jolla Biological Laboratory aided in taking the series, including Ralph Silliman, John C. Marr, Oscar E. Sette, James R. Thraillkill, Robert C. Counts, David Kramer, Robert Livingstone, and Bruce Taft. The figures were prepared by Andrew M. Vrooman. I wish to thank David Kramer for helpful suggestions during preparation of the manuscript.

SOME GENERAL OBSERVATIONS ON DEPTH DISTRIBUTION

Before discussing the vertical distributions of individual species, some general observations will be given on depth distribution. The average weighted depth distributions of the 15 most common kinds of larvae taken in vertical distribution series are summarized in table 4. In these determinations, the depth of the zone represented by each level in the series is taken into account.

Larvae may be divided into two principal groups with respect to depth distribution: (1) Those species occurring almost entirely within the upper mixed layer and in the upper part of the thermocline; (2) those species occurring mostly within or below the thermocline.

Of the 15 kinds of larvae summarized in table 4, 12 fall into the first category and 3 into the second.

Many of the differences in the depth distribution of larvae of the same species in the various series are due to differences in the position of the thermocline. The extremes in thermocline depth were found at stations 5206-90.28N and 5504-110.60. In the former, only the two shallowest tows at average depths of 2 and 7 meters were taken in the layer above the thermocline, the hauls taken at approximately 17 and 27 meters deep were within the zone of rapid temperature decline, and the haul averaging 42 meters deep was definitely below the thermocline. At station 5504-110.60, on the other hand, there was a dif-

TABLE 4.—Average weighted depth distributions of the 15 most common kinds of larvae taken in vertical distribution series

Species	Percentage occurrence of larvae at—						Total
	0-23 meters	24-48 meters	49-64 meters	65-88 meters	89-122 meters	Below 122 meters	
Group I: ¹							
<i>Pneumatophorus diego</i>	79.4	19.9	0.7	0	0	0	100.0
<i>Sardinops caerulea</i>	47.1	32.3	5.8	14.8	0	0	100.0
<i>Trachurus symmetricus</i>	40.9	38.1	7.4	10.0	3.6	0	100.0
<i>Engraulis mordax</i>	38.0	46.0	11.7	3.3	.1	0	100.0
<i>Vinciguerria lucetia</i>	16.2	46.8	7.8	20.6	8.7	0	100.1
<i>Sebastodes</i> spp.....	14.5	41.2	24.7	16.1	3.5	0	100.0
<i>Citharichthys</i> spp.....	12.6	70.6	14.4	2.4	0	0	100.0
<i>Lampanyctus leucopsarus</i>	4.4	55.8	32.3	5.7	1.7	0	99.9
<i>Lampanyctus mexicanus</i>	5.9	45.6	29.6	15.2	2.2	1.5	100.0
<i>Lampanyctus ritleri</i>	3.8	43.6	27.8	20.5	4.4	0	100.1
<i>Tarletonbeania crenularis</i>	0	31.7	42.3	8.8	12.1	5.0	99.9
<i>Diogenichthys laternatus</i>	0	2.2	1.8	73.0	23.0	0	100.0
Group II: ²							
<i>Merluccius productus</i>	1.5	3.5	14.0	47.5	10.6	22.9	100.0
<i>Bathylagus wesethi</i>3	.8	7.4	25.6	50.0	16.0	100.1
<i>Leuroglossus stilbius</i>4	5.1	13.2	18.0	18.9	44.4	100.0

¹ Distribution confined to upper mixed layer.

² Distribution mostly within or below thermocline.

ference of only 0.3° C. between the temperature at the surface and that at 83 meters deep (the average depth of the horizontal haul taken with 125 meters of towing cable payed out). The thermocline began at a depth of approximately 90 meters at this station. Since the vertical distributions of most larvae are confined to the upper mixed layer and the upper portion of the thermocline, their depth distributions are shallow in situations such as that sampled at 5206-90.28N, and deeper and more varied at stations having a deep thermocline.

Some differences in depth distribution are due to diurnal changes in level associated with phototropic response of larvae to light (usually negative). Vertical movements of larvae are apparently limited in extent, being confined for most kinds to movements within the upper mixed layer. There is no evidence that fish larvae move through the thermocline while making diurnal vertical movements.

Most kinds of fish larvae are confined in their vertical distribution to the upper mixed layer and the upper portion of the thermocline. However, within the upper mixed layer the various kinds of larvae have different but characteristic depth distributions. Several species occurred in greatest abundance in the upper 23 meters of depth at most stations. Included in this group are *Pneumatophorus diego* (fig. 3, b), *Sardinops caerulea* (fig. 2, a), and *Trachurus symmetricus* (fig. 3, c). The anchovy, *Engraulis mordax*, although it occurred mostly in the upper 23-meter level at some stations, was found on the average to be somewhat more abundant in the level between 24 and 48 meters (fig. 2, b). *Sebastes* larvae were uncommon in the upper level (0-23 meters) at most stations (fig. 3, d), but they occurred in greatest abundance in this level in one night series. Larvae of *Vinciguerria lucetia* (fig. 2, c) and *Citharichthys* spp. (fig. 3, a) had their largest concentrations in the 24- to 48-meter level.

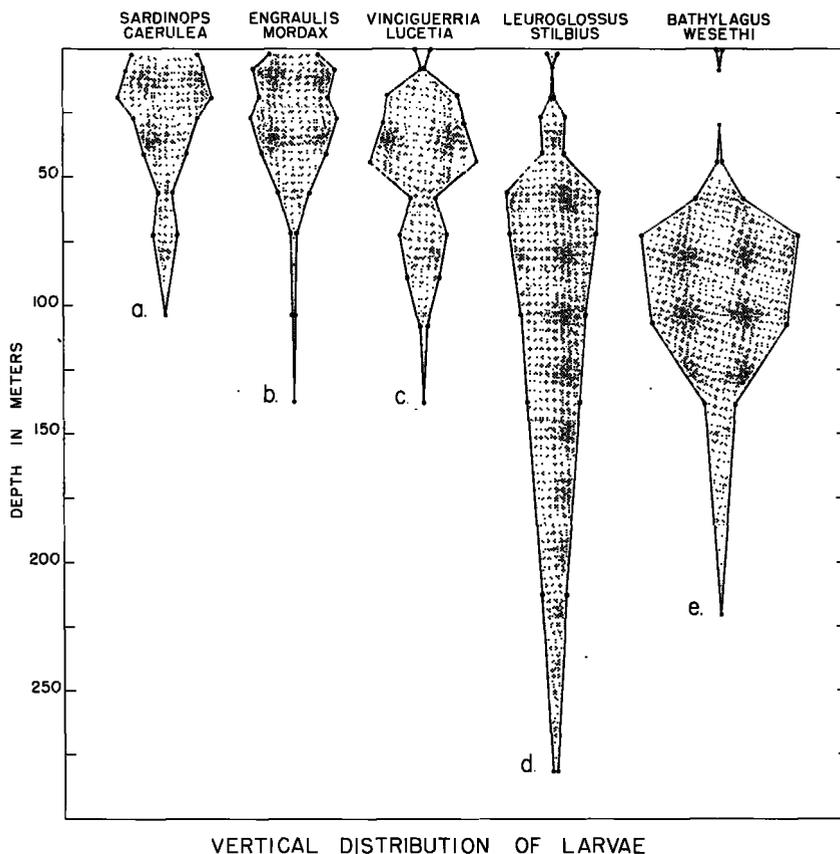


FIGURE 2.—Weighted average vertical distribution of larvae of (a) *Sardinops caerulea*, (b) *Engraulis mordax*, (c) *Vinciguerria lucetia*, (d) *Leuroglossus stilbius*, and (e) *Bathylagus wesethi*.

Myctophid larvae were not taken in any numbers in the 0–23 meter level, but usually had their centers of abundance between 24 and 64 meters (fig. 12). Larvae of *Diogenichthys laternatus* had a somewhat deeper distribution (fig. 12, e), but they still were confined to the upper mixed layer (the thermocline was deep at each station where this species was collected).

The larvae of three species occurred in greatest abundance within and below the thermocline: *Merluccius productus* (fig. 3, e), *Leuroglossus stilbius* (fig. 2, d), and *Bathylagus wesethi* (fig. 2, e). All of these species occurred at somewhat lower temperatures than larvae confined to the upper mixed layer. It is likely that temperature is a more important factor than pressure in the depth distribution of these species.

If these series are representative samplings of the depth distributions of fish larvae, it follows that the complete depth range of the larvae of most species could be completely encompassed by

hauls averaging approximately 125 meters deep. In making plankton hauls on CCOFI cruises, the net is hauled obliquely from approximately 140 meters deep to the surface (depth of water permitting), hence the depth distribution of most kinds of fish larvae would be encompassed by these hauls.

DEPTH DISTRIBUTIONS OF INDIVIDUAL SPECIES

Pacific Sardine (*Sardinops caerulea*)

Larvae of the sardine were taken in 17 series, eggs in only 7 (table 5). The vertical distributions of sardine eggs and larvae have been discussed by Silliman (1943) and Ahlstrom (1948). Silliman included several series in his account that are not included here (series taken in 1939 that do not conform to spacing in subsequent series). All series taken subsequent to 1941 have not been reported upon previously.

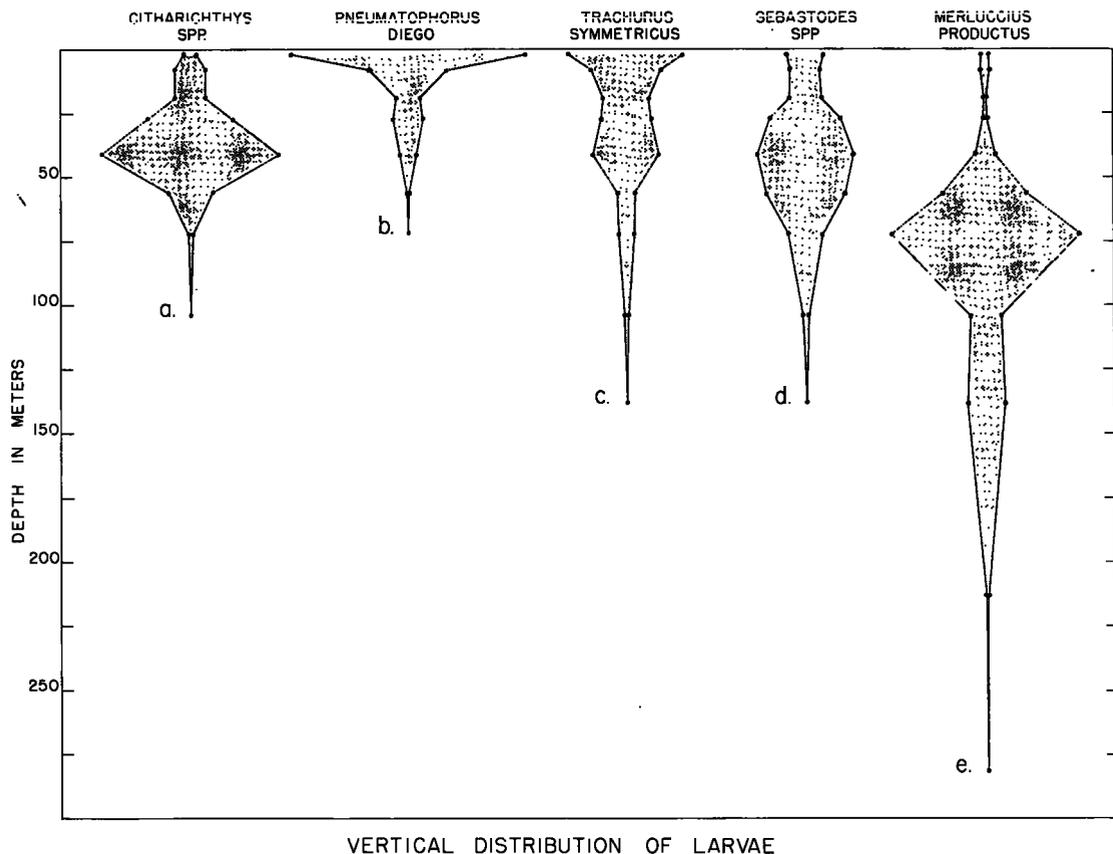


FIGURE 3.—Weighted average vertical distributions of larvae of (a) *Citharichthys* spp., (b) *Pneumatophorus diego*, (c) *Trachurus symmetricus*, (d) *Sebastodes* spp., and (e) *Merluccius productus*.

TABLE 5.—Depth distributions of larvae and eggs of Pacific sardine, *Sardinops caerulea*

Station series	Number per haul at average depth (m.) of—												Total
	2	8	19	28	41	56	72	88	105	138	215	285	
Larvae:													
4104-91.54	90	179	195	121	117	31	1		0				784
4105-89.38	0	0	0	32	2	0	0		0				34
4105-92.39	410	248	10	7	1	0	0		0				676
4106-94.37N	21	3	12	1	3	0	0		0				40
4106-94.37D	0	0	0	1	2	2	1		0				6
4106-94.47N	14	13	23	35	4	0	0		0				89
4106-94.47D	5	0	6	9	2	2	0		0				24
4106-97.43N	1	0	0	0	0	0	0		0				1
5206-90.28N	3	2	0	0	0	0	0		0	0	0	0	5
5206-90.28D	0	3	0	0	0	0	0		0	0	0	0	3
5208-120.35	10	65	15	17	7	0							114
5403-94.80N	0	1	1	5	2	2	0		0	0	0	0	10
5403-94.80D	0	0	0	0	1	1	2		0	0	0	0	4
5504-107.80	1	0	19	6	5	0	1		3	0	0	0	35
5504-110.60	0	0	0	0	23	10	24		2	0	0	0	59
5504-120.50	2	1	0	2	2	0	0		0	0	0	0	7
5504-130.60	1	0	0	0	0	0	0		0	0	0	0	1
Total	558	514	281	236	171	48	29	5	0	0	0	0	1,842
Eggs:													
4105-92.39	90	16	1	1	0	0	0		0				108
5206-90.28N	4	0	2	0	0	0	0		0	0	0	0	6
5206-90.28D	2	0	1	0	0	0	0		0	0	0	0	3
5208-120.35	22	17	33	35	40	5							152
5403-94.80N	37	29	46	50	65	33	11		0	0	0	0	271
5403-94.80D	59	51	29	20	21	11	7		3	0	0	0	201
5504-120.50	0	2	0	0	0	0	0		0	0	0	0	2
Total	214	115	112	106	126	49	18	0	3	0	0	0	743

The depth range of sardine larvae in vertical distribution series is from 0 to approximately 96 meters, and the eggs range from 0 to approximately 121 meters. I wish to clarify a usage in defining the limits of depth ranges in this and subsequent discussions of other species. When indicating the depth range of sardine larvae, I have given the deeper limits of the level, whose average depth is 88 meters. Similarly, sardine eggs were taken in a haul having an average depth

of 105 meters; the deeper limit of this stratum is approximately 121 meters.

The depth distributions of sardine larvae in individual series are illustrated in figure 4. In two series, the larvae were concentrated into a rather narrow zone. Thus, at station 4105-92.39 (fig. 4, a), most larvae occurred in the upper two hauls of the series, and at station 5208-120.35 (fig. 4, b), a marked concentration occurred at the 10-meter level. At station 4104-91.54 (fig.

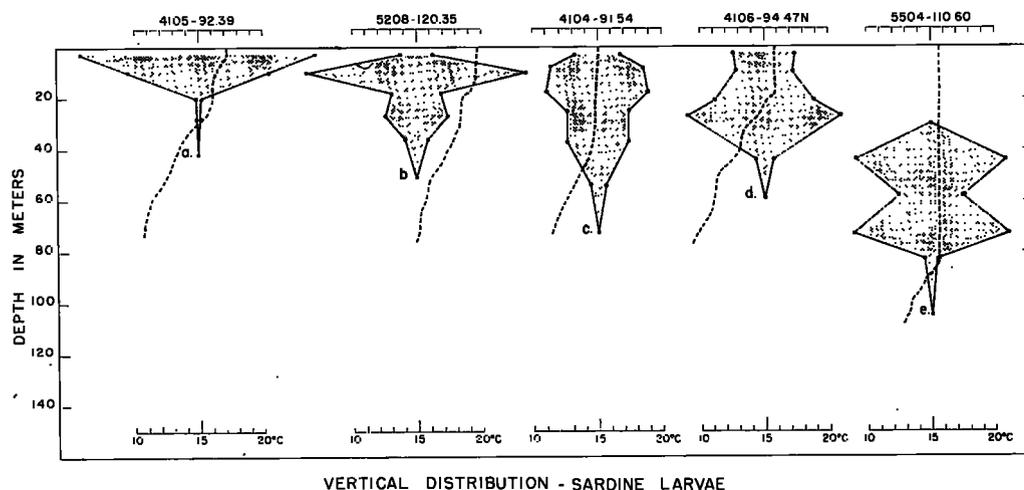


FIGURE 4.—Vertical distributions of sardine (*Sardinops caerulea*) larvae in five separate series, with superimposed temperature profiles.

4, c), however, the larvae were rather similar in numbers at four levels between 8 and 37 meters in average depth. In 4 of the 5 series illustrated in figure 4 the larvae were found almost entirely above 50 meters deep. Three of these were night series, the fourth (4104-91.54) was started in the afternoon and completed after dark. In the single day series illustrated, 5504-110.60 (fig. 4, e), the larvae occurred mostly below 50 meters, in the lower half of the upper mixed layer. The thermocline was deeper at this station than at most other stations at which depth distribution studies were made. Differences in depth distributions of sardine larvae in day and night series are discussed in a following section.

The average weighted depth distribution of sardine larvae, based on vertical distribution series, had the following percentages in different depth strata:

Strata:	Percentage of total
0-23 meters-----	47.1
24-48 meters-----	32.3
49-64 meters-----	5.8
65-88 meters-----	14.8
89 meters and below-----	0

A somewhat shallower distribution was indicated in studies reported by Ahlstrom (1948). Two to three closing nets were used in series at most stations in 1939; the upper net fished from approximately 42 meters to the surface, the intermediate net from 81 to 38 meters, and the bottom net from 120 to 72 meters. The exact depth fished by each net varied from haul to haul. About 93 percent of the sardine larvae were taken in the upper level, 7 percent in the intermediate level, and none in the lowest level. A closing net was used below the upper net at 133 stations occupied in 1940. It sampled the zone between approximately 130 and 57 meters. Less than 1 percent of sardine eggs and larvae were taken in the deeper stratum. Inasmuch as the 1939 and 1940 studies represent a larger number of observations than the vertical distribution series, they may reflect the average depth distribution of sardine larvae more adequately than the weighted distributions given above.

Water temperatures at the levels where sardine larvae were collected ranged from 10.9° to 19.7° C. Only 17 larvae were taken at temperatures lower than 13.0° C. The only series in which water temperatures were above 17.0° C. was at sta-

tion 5208, taken during August in Sebastian Viscaïno Bay, central Baja California. This series represents offseason sardine spawning, which centers in the Sebastian Viscaïno Bay area. This spawning occurs at considerably higher temperatures than during the regular spawning season, and there is a possibility that the offseason spawners may belong to a separate subpopulation of sardines.

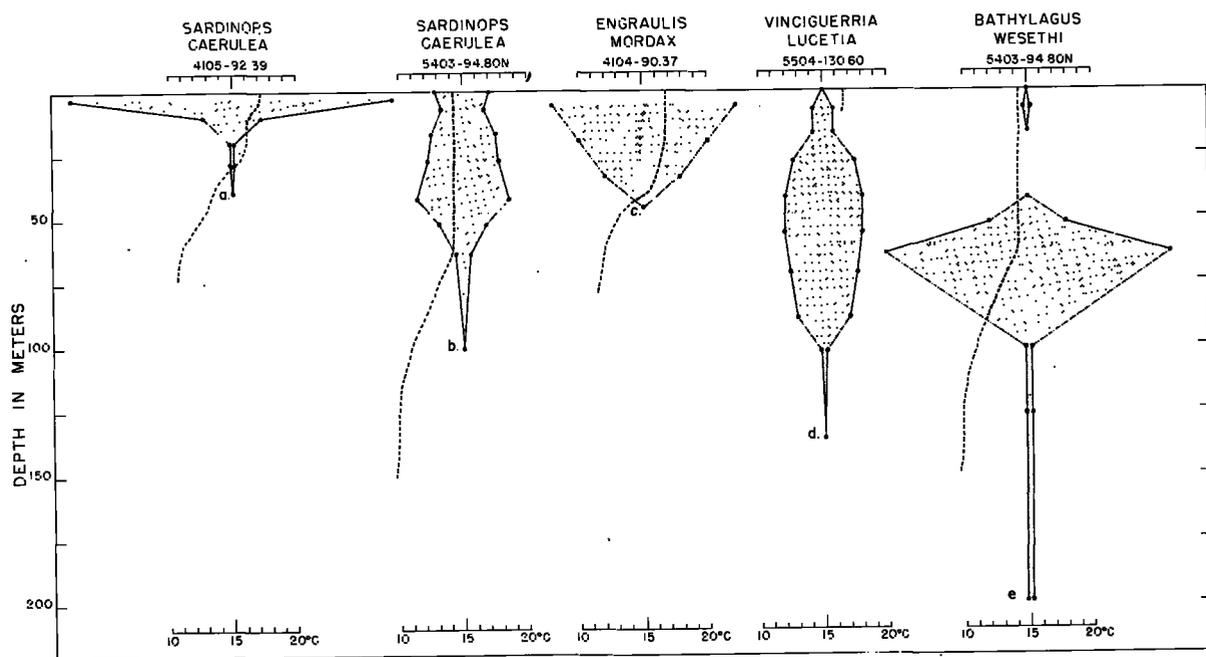
Two contrasting distributions are illustrated for sardine eggs. At station 4105-92.39 (fig. 5, a) most of the eggs were taken in the surface haul. The depth distribution of sardine eggs at this station is fairly similar to the distribution of sardine larvae (fig. 4, a). A higher percentage of sardine eggs than larvae occurred in the surface haul, but both categories have a very shallow depth distribution. Sardine eggs occurred over a fairly wide depth zone at station 5403-94.80N (fig. 5, b): from the surface to approximately 82 meters, with the largest concentration (23 percent of the total) at 42 meters. The few sardine larvae obtained in this series occurred at depths between 14 and 64 meters.

Northern Anchovy (*Engraulis mordax*)

Anchovy larvae were the most abundant kind taken in depth distribution studies: they were present in 18 of the 22 series, and were very common to very abundant (125 to 5,144 per series) in half of these (table 6). The weighted average vertical distribution of anchovy larvae is illustrated in figure 2, b.

The depth distributions of anchovy larvae in five series are illustrated in figure 6. Three of these series were made at night, two during daytime. The two daytime series have contrasting distributions. At station 4105-89.38 (fig. 6, d), most larvae were taken at one level (25 meters), while at station 5504-107.80 (fig. 6, e), the larvae were deeper and more dispersed. The thermocline was shallow at station 4105-89.38; there was a temperature drop of 3.3° C. between the 25- and 56-meter level. The thermocline was deep at station 5504-107.80; there was only 0.7° C. difference between the temperature at the surface and that at 70 meters.

Anchovy larvae were unusually abundant at station 5504-120.50; in fact the 5,144 anchovy larvae taken at this station constitute about 28 percent of all larvae taken in vertical distribution series. Anchovy larvae had a wide depth range



VERTICAL DISTRIBUTION OF EGGS AT INDIVIDUAL STATIONS

FIGURE 5.—Vertical distributions of the eggs of four species of fish at individual stations. Species and station numbers are listed above each diagram and a temperature profile is superimposed.

at this station, from 0 to approximately 125 meters. The largest concentrations were in the two shallowest hauls, but larvae were abundant to approximately 66 meters.

Additional information on depth distribution of anchovy larvae is available from the 1940 survey, when a closing net fishing from approxi-

mately 130 to 57 meters was used at most stations below the upper net. The number of anchovy larvae obtained from 133 closing-net hauls was 148, as compared to 5,940 larvae in the upper net hauls at the same stations. Thus, only about 2½ percent of the larvae were distributed as deeply as 57 meters. It is interesting to note that only

TABLE 6.—Depth distributions of larvae and eggs of northern anchovy (*Engraulis mordax*)

Station series	Number per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
Larvae:													
4104-91.54	3	4	4	62	248	21	0						342
4105-89.38	0	1	7	148	9	4	0						169
4105-92.39	231	247	36	53	10	0	0		0				577
4106-94.37N	4	8	6	5	4	0	0						27
4106-94.37D	0	0	0	1	1	2	0		0	0			4
4106-94.47N	7	5	61	114	30	0	0		0				217
4106-94.47D	1	2	0	0	4	2	1		0	0			10
4106-97.43N	1	1	4	6	0	0	0		0	0			12
5206-90.28N	196	205	114	97	0	0	0		0	0	0	0	612
5206-90.28D	5	136	9	0	1	0	0		0	0	0	0	151
5208-120.35	4	30	19	19	46	7							125
5303-91.38N	1	1	4	6	0	0	0		0	0	0	0	12
5305-93.50N	8	0	2	0	0	0	0		0	0	0	0	10
5305-93.50D	0	0	2	8	4	6	0		0	0	0	0	20
5504-107.80	4	0	0	19	159	271	73	16	1	0			543
5504-110.60	14	0	0	0	0	1	0	0	0	0			15
5504-120.50	1,370	1,405	837	270	697	488	72	4	1	0	0	0	5,144
5504-130.60	0	0	0	1	0	0	0	0	0	0	0	0	1
Total	1,849	2,045	1,105	809	1,213	802	146	20	2	0	0	0	7,991
Eggs:													
4105-89.38	246	30	0	9	0	2	0						287
5206-90.28N	0	0	1	0	0	0	1		0	0	0	1	3
5206-90.28D	43	4	1	0	0	1	1		4	2	9	4	69
Total	289	34	2	9	0	3	2		4	2	9	5	359

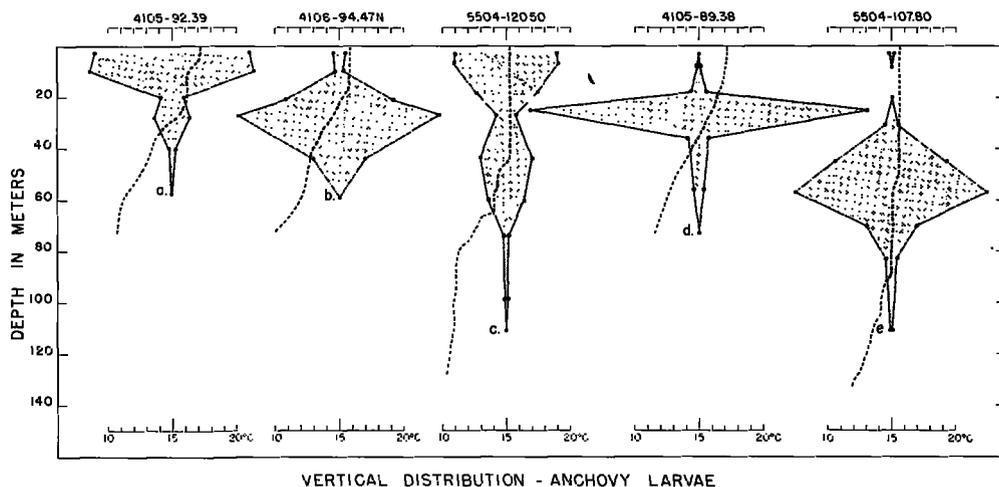


FIGURE 6.—Vertical distributions of anchovy (*Engraulis mordax*) larvae in five separate series, with superimposed temperature profiles.

11 larvae were taken in closing net hauls made at night, while 137 were taken in day hauls. A deeper distribution in day hauls was also found in replicate vertical series, discussed in a latter section.

Anchovy larvae were taken over a wide temperature range, 10.0° to 19.7° C. Most larvae occurred within a 3.5° -temperature range, 14.0° to 17.4° C., however; approximately 95 percent of the total number of anchovy larvae were obtained within this temperature range. Only nine larvae were taken at temperatures below 12.0° C., and occurrences above 17.5° C. were mostly from station 5208-120.35 in Sebastian Viscaino Bay.

Anchovy and sardine larvae had fairly similar depth distributions at most stations where they both occurred. Their depth distributions at stations 4105-92.39 and 4106-94.47N are shown in figure 4, a and d, for sardine larvae, and figure 6, a and b, for anchovy larvae. In both series the two species have similar depth ranges, but a somewhat larger portion of the sardine larvae was taken in the shallower hauls. There is a more

marked contrast in the depth distributions of the two species at station 4104-91.54. In this series nearly three-fourths of the anchovy larvae were taken in the fifth haul of the series, averaging 36 meters (not illustrated), while the center of abundance of sardine larvae was much shallower (fig. 4, c).

There is limited information on the depth distribution of anchovy eggs, which were taken in only three of the regular series. In these series (table 6), 90 percent of the eggs were taken in the two shallowest hauls of each series, but some eggs were obtained throughout the depth range sampled. The presence of eggs in the deeper hauls made at station 5206-90.28 is difficult to explain, since anchovy larvae were not taken at these depths either at this station or in any other series.

Silliman (1943) made use of five vertical series (F8A, F8B, F9A, F9B taken in 1939, and 1832 taken in 1941) that are not included in the present report. Inasmuch as anchovy eggs were taken in three of these series, the information is given below:

Series F8A			Series F8A			Series 4104-90.37 (1832)		
Middepth of haul	Number of eggs	Temperature ($^{\circ}$ C.)	Middepth of haul	Number of eggs	Temperature ($^{\circ}$ C.)	Middepth of haul	Number of eggs	Temperature ($^{\circ}$ C.)
2 m.....	35	15.4	4 m.....	2,552	15.6	6 m.....	47	16.8
7 m.....	7	15.3	13 m.....	194	15.3	20 m.....	32	16.7
12 m.....	12	15.2	30 m.....	65	11.7	34 m.....	18	15.9
22 m.....	0	14.5	51 m.....	1	10.3	46 m.....	0	13.7
32 m.....	1	11.9	57 m.....	11	10.2	58 m.....	0	12.3
45 m.....	0	10.7				77 m.....	0	11.5
55 m.....	0	10.2						
111 m.....	2	9.5						

As in the series discussed above, the largest concentrations of eggs occurred in the upper haul of each series. The distribution in series 4104-90.37 (1832) is illustrated in figure 5c.

Information on the depth distribution of anchovy eggs within the upper 40-meter level based on material from high-speed sampler hauls is available for six sets of hauls (Ahlstrom et al. 1958). In the three sets containing the largest number of eggs, the majority were taken below 20 meters. Hence there is more variation in depth distribution of eggs than was indicated in the vertical distribution series.

It is interesting to note the differences in depth distribution of anchovy eggs and larvae at station 4105-89.38. Nearly 86 percent of the anchovy eggs were taken in the surface haul, while as large a percentage of the larvae was taken in the haul averaging 25 meters deep (fig. 6, d). Most of the larvae were under 4 millimeters in length, hence too small to participate in any marked vertical movement. The only fins developed on 4-millimeter anchovy larvae are larval pectorals.

Jack Mackerel (*Trachurus symmetricus*)

The majority of vertical distribution series were not taken in areas where jack mackerel larvae commonly occur. The center of abundance of jack mackerel larvae is usually between 80 and 240 miles offshore (Ahlstrom and Ball, 1954: 227),

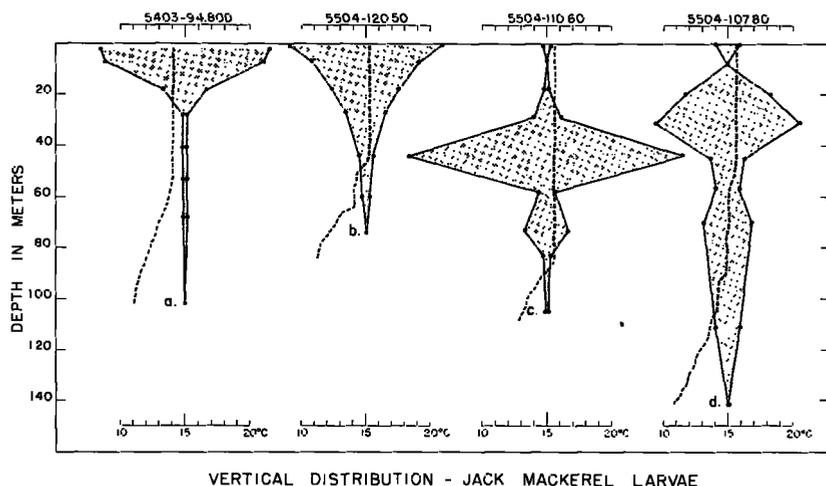
while most vertical series were taken within 80 miles of the coast. Jack mackerel larvae were taken in 13 series (table 7), but occurred in small numbers (1 to 7 larvae per series) in nearly half of the series, and commonly (50 or more per series) in only five series.

The larvae were taken between the surface and approximately 122 meters, although approximately four-fifths of the larvae occurred within the upper 50 meters (fig. 3, c). Considerable variation was found from series to series, as is shown in figure 7. Jack mackerel larvae decreased in abundance with depth at station 5504-120.50 (fig. 7, b), were mostly concentrated within the upper 10 meters at station 5403-94.80D (fig. 7, a), had a marked center of abundance at 44 meters at station 5504-110.60 (fig. 7, c), and had a wide depth range at station 5504-107.80 (fig. 7, d).

The depth distributions of jack mackerel eggs are illustrated in figure 8. The same series are shown for eggs as for larvae, with the addition of station 5403-94.80N. The secondary concentration of eggs, which occurred at a depth of 42 meters at the latter station (fig. 8, c) resulted from eggs spawned during the night of collection. Of the 346 jack mackerel eggs taken in this haul, 338 were recently spawned. Most of the newly spawned eggs (321) had not yet initiated cleavage, hence spawning may have occurred within the hour. This haul was taken at about 11 p.m.

TABLE 7.—Depth distributions of larvae and eggs of jack mackerel (*Trachurus symmetricus*)

Station series	Number per haul at average depth (m.) of—												Total
	2	8	19	28	41	56	72	88	105	138	215	285	
Larvae:													
4104-91.54	2	0	1	1	0	0	0	0	0	0	0	0	4
4105-92.39	10	9	1	1	0	0	0	0	0	0	0	0	21
4106-94.37D	0	0	0	0	1	0	0	0	0	0	0	0	1
4106-94.47N	0	0	4	3	0	0	0	0	0	0	0	0	7
5206-90.28N	12	13	0	0	1	0	0	0	0	0	0	0	26
5206-90.28D	0	2	0	0	0	0	0	0	0	0	0	0	2
5305-93.50N	0	4	0	0	0	0	0	0	0	0	0	0	4
5305-93.50D	0	0	0	0	2	0	0	0	0	0	0	0	2
5403-94.80N	26	0	5	7	6	8	0	0	0	0	0	0	52
5403-94.80D	92	86	24	2	2	2	2	0	0	0	0	0	210
5504-107.80	4	0	14	24	6	4	8	8	4	0	0	0	73
5504-110.60	6	0	3	25	209	13	34	6	1	0	0	0	297
5504-120.50	34	24	15	9	3	1	0	0	0	0	0	0	86
Total	186	138	67	72	230	28	44	14	5	0	0	0	784
Eggs:													
5403-94.80N	602	51	32	54	346	25	6	0	1	0	0	0	1,117
5403-94.80D	1,017	822	265	38	30	11	6	7	0	0	0	0	2,196
5504-107.80	36	19	11	30	10	4	11	0	0	0	0	0	121
5504-110.60	54	11	27	4	7	6	21	3	1	0	0	0	134
5504-120.50	29	38	24	1	0	0	0	0	0	0	0	0	92
Total	1,738	941	359	127	393	46	44	3	8	1	0	0	3,680



VERTICAL DISTRIBUTION - JACK MACKEREL LARVAE

FIGURE 7.—Vertical distributions of jack mackerel (*Trachurus symmetricus*) larvae in four separate series, with superimposed temperature profiles.

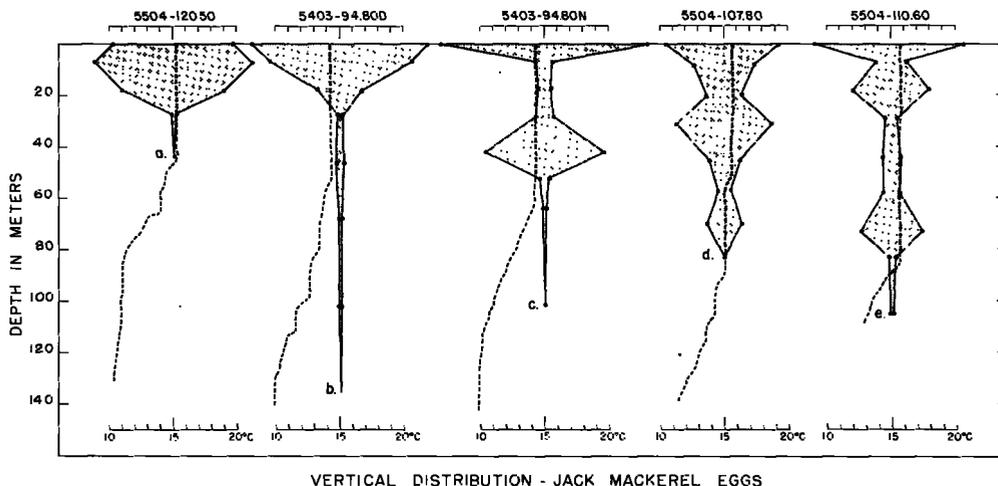
The distribution of recently spawned eggs at this station is shown in the following tabulation:

Average depth of haul	Number of jack mackerel eggs		
	Recently spawned	Middle and late stage	Total
2 meters.....	0	602	602
7 meters.....	2	49	51
17 meters.....	3	29	32
27 meters.....	36	18	54
42 meters.....	338	8	346
52 meters.....	6	19	25
64 meters.....	1	5	6
101 meters.....	0	0	0

Some newly spawned eggs were taken at other depths, especially in the haul averaging 27 meters in depth. If the depth of occurrence of newly spawned eggs can be assumed to reflect the

depth at which spawning took place, then in this instance, at least, spawning occurred below the level of abundance of the older eggs. Two possible explanations of this difference in distribution are that the older eggs had changed their depth distribution since spawning by floating upward, or that spawning had occurred at shallower depths on the preceding several nights. I consider the latter explanation to be the more likely.

There are interesting similarities and differences in the depth distributions of eggs and larvae. The distributions of eggs and larvae in series 5403-94.80D are quite similar; their distributions in series 5504-110.60 are markedly different. In the latter series, only about 3 percent



VERTICAL DISTRIBUTION - JACK MACKEREL EGGS

FIGURE 8.—Vertical distributions of jack mackerel (*Trachurus symmetricus*) eggs in five separate series, with superimposed temperature profiles.

of the larvae were taken in the upper three hauls, while nearly 69 percent of the eggs were taken in these hauls. In the two other series that are illustrated, the eggs also have a somewhat shallower distribution than the larvae. At station 5504-107.80, about 45 percent of the eggs were taken in the two shallowest hauls and only 6 percent of the larvae.

Jack mackerel larvae were taken within a 4°-temperature range, 13.0°-16.9° C., except for one occurrence at 10.1° C. The great majority of larvae occurred within a 2° range, 14.0°-15.9° C. The eggs had an even more restricted range: 99.6 percent of the eggs occurred at temperatures between 14.0° and 15.7° C. These observations agree well with those given in table 10 of Ahlstrom and Ball (1954), who found that over 70 percent of the larger collections of larvae (50 or more per standard haul) occurred within the 2°-temperature range noted above (14°-16° C.). The authors were dealing with a much larger mass of data—780 collections of larvae made in 1950 to 1952—hence it is not surprising that they found a wider temperature range, 10.0°-19.5° C., for the larvae in these collections.

Pacific Mackerel (*Pneumatophorus diego*)

Pacific mackerel larvae were obtained in only three series (table 8). None of the larvae occurred below approximately 66 meters deep, and nearly 80 percent of them occurred in the 0- to 23-meter level. This is the shallowest depth distribution found for any of the more common kinds of larvae. The temperature range at which larvae occurred was between 14.1° and 17.1° C. The weighted average depth distribution of larvae is shown in figure 3, b, the distributions at individual stations are shown in figure 9, a and b.

Inasmuch as Pacific mackerel larvae were not taken in any vertical series where the upper mixed layer was deep, it is probable that a somewhat deeper distribution would be found in these situations. Pacific mackerel larvae are taken in such situations on regular survey cruises.

Pacific mackerel eggs, which occurred in abundance at station 5504-120.50, had a less restricted depth distribution than the larvae (fig. 9, c).

Hake (*Merluccius productus*)

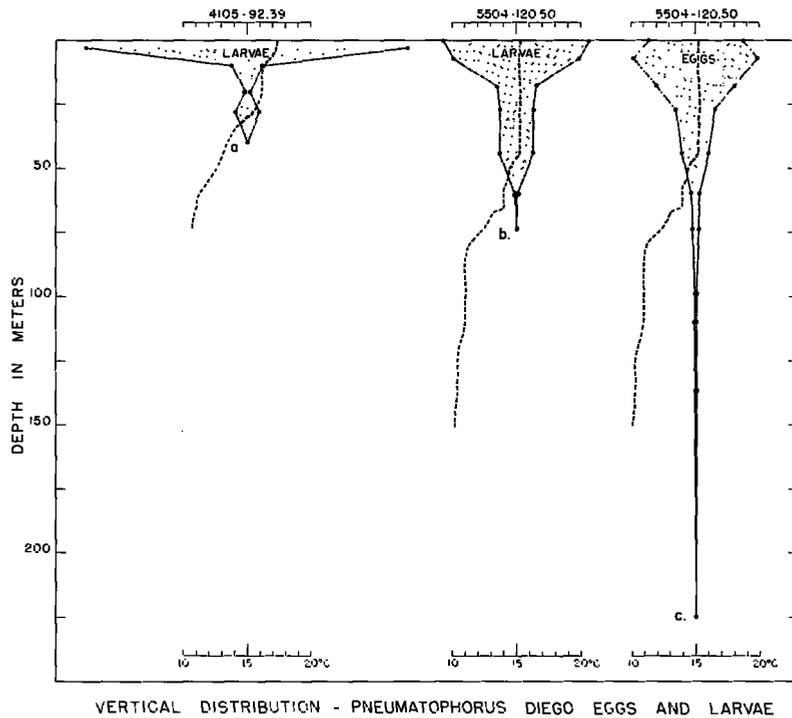
Hake larvae rank second in abundance to anchovy, both in yearly summaries of larvae in the COCOFI survey area and in the vertical distribution series. Hake larvae were taken in 13 series, commonly in 4; hake eggs in 6 series, commonly in 2 (table 9). Some of the data on vertical distribution of hake larvae have already been given in Ahlstrom and Counts (1955: 315).

Hake larvae were taken mostly within or below the thermocline. Only 5 percent of the larvae were obtained between the surface and 48 meters (table 4). In three of the four series in which hake larvae were common, the center of abundance occurred in the haul at an average of 72 meters deep (fig. 10, a, b, and d), and very few larvae were taken below 122 meters.

A deeper distribution of larvae was obtained at station 5504-107.80. Unfortunately, this is an incomplete series, with the deepest haul averaging 142 meters in depth. Hake larvae were taken in the six hauls made between 45 and 142 meters, with an increase in abundance with depth. Nearly 38 percent of the larvae were taken in the bottom haul of this series. Depth distribution at this station is so different from the others, that it points up the incompleteness of our depth distribution data for this species and the need for additional series.

TABLE 8.—Depth distributions of larvae and eggs of Pacific mackerel (*Pneumatophorus diego*)

Station series	Number per haul at average depth (m.) of—												Total
	2	8	19	28	41	56	72	88	105	128	215	285	
Larvae:													
4105-92.39.....	52	5	1	4	0	0	0	0	0	0	0	0	62
4106-94.47N.....	1	0	6	1	0	0	0	0	0	0	0	0	8
5504-120.50.....	56	48	15	13	14	1	0	0	0	0	0	0	147
Total.....	109	53	22	18	14	1	0	0	0	0	0	0	217
Eggs: 5504-120.50.....	544	721	450	221	164	51	35	13	13	9	0	0	2,221
Total.....	544	721	450	221	164	51	35	13	13	9	0	0	2,221



VERTICAL DISTRIBUTION - PNEUMATOPHORUS DIEGO EGGS AND LARVAE

FIGURE 9.—Vertical distributions of Pacific mackerel (*Pneumatophorus diego*) larvae and eggs in separate series, with superimposed temperature profiles.

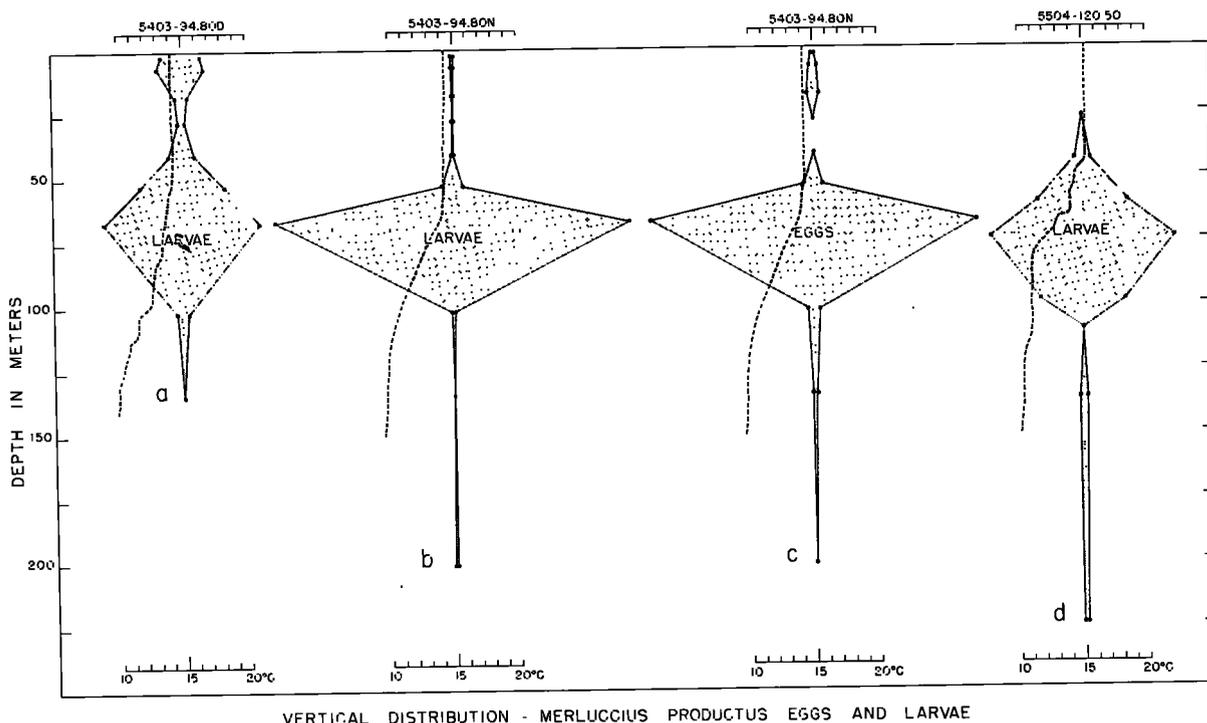
In vertical series, hake larvae were taken at temperatures between 8.7° and 15.7° C., with most occurring between 10.6° and 15.0° C. Interestingly, Ahlstrom and Counts (1955:328) found that larger concentrations of hake larvae (1,001 or more per standard haul) taken on survey

cruises occurred within this identical 4½° temperature range.

Hake eggs were common only in the two series (N and D) taken at station 5403-94.80. The distribution of hake eggs in the series taken at night (fig. 10, c) is strikingly similar to the dis-

TABLE 9.—Depth distributions of larvae and eggs of hake (*Merluccius productus*)

Station series	Number per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
Larvae:													
4104-01.54	0	0	0	0	3	20	13						36
4105-89.38	0	0	0	0	0	14	7		0				21
4105-92.39	0	0	0	3	5	9	4		1				22
4106-94.37N	0	0	0	0	2	0	1		0				3
4106-94.47N	0	0	0	1	3	4	0		0	0			8
4106-97.43N	0	0	0	0	0	0	0		0	1			1
5303-01.38N	0	0	0	0	0	8	12		0		0	0	20
5303-01.38D	0	0	0	0	3	2	0		0	0	0	0	5
5403-94.80N	15	6	5	1	2	93	1,622		8	0	1		1,753
5403-94.80D	69	86	24	14	49	156	287		22	0	0		707
5504-107.80	0	0	0	0	1	4	31	38	59	81			214
5504-110.80	0	0	0	0	0	0	0	0	2				2
5504-120.50	0	0	0	0	4	23	48	22	0	2	1		100
Total	84	92	29	19	72	333	2,025	60	92	84	2	0	2,892
Eggs:													
5303-01.38N	2	0	0	2	1	0	0		0	0	0	0	5
5303-01.38D	0	0	0	1	0	0	0		0	0	0	0	1
5403-94.80N	1	2	3	0	0	5	87		3	1	0		102
5403-94.80D	2	0	0	2	7	22	69		0	0	2		101
5504-107.80	0	0	0	0	8	2	1	4	0	0			15
5504-120.50	0	0	0	0	0	0	0	0	1	2	0		3
Total	5	2	3	5	16	29	154	4	4	3	2		227



VERTICAL DISTRIBUTION - MERLUCCIIUS PRODUCTUS EGGS AND LARVAE

FIGURE 10.—Vertical distributions of Hake (*Merluccius productus*) larvae and eggs in separate series, with superimposed temperature profiles.

tribution of larvae in the same series (fig. 10, b). Almost identical numbers of eggs were taken in these day and night series, although there was not as marked a concentration of the eggs at one depth in the day series as in the night. A few (15) hake eggs were taken at station 5504-107.80; they were taken in the four contiguous hauls made between 41 and 88 meters, but no eggs were taken in the two lower hauls of this series; hence, the depth distribution of eggs at this station was shallower than the distribution of larvae.

Rockfish Larvae (*Sebastes* spp.)

The category of rockfish larvae is restricted to a single genus, *Sebastes*, containing a number of species. Larvae of *Sebastes* can be identified to genus without difficulty, but no attempt has been made to extend identification to the specific level. According to Phillips (1957), 49 species of *Sebastes* occur off California, and 34 of them are definitely known to occur off Baja California, as well.

Rockfish larvae usually are taken in a larger number of plankton hauls on CCOFI cruises than any other kind of larva. This wide distribution

is also reflected in their frequency of occurrence in vertical distribution series. Rockfish larvae were taken in 17 series, and in all but 1 of these, 15 or more larvae were taken per series (table 10).

Rockfish larvae were seldom common in the upper 23 meters (figs. 3, d, and 11, a to d). Usually the largest numbers were taken in hauls averaging 28, 41, and 56 meters deep. However, at station 5305-93.50N (fig. 11, a) the largest number was taken in the surface haul, and at station 5504-120.50 (fig. 11, d) there were two levels of concentration, one near the surface, the other at 72 meters deep. Only nine rockfish larvae were taken below 100 meters, all of these occurring in hauls averaging 105 meters deep. Thus, rockfish larvae belong to the large group of fish larvae that occurs in the upper mixed layer or within the thermocline, but not below it.

Sebastes larvae were taken at temperatures between 9.0° and 17.2° C., with the larger concentrations occurring at temperatures between 10.2° and 16.1° C. At individual stations, the temperature ranges over which larvae were taken was as great as 5.7° C. (series 4105-89.38 and 4105-92.39). In about half of the series the largest

TABLE 10.—Depth distributions of larvae of rockfishes (*Sebastes* spp.)

Station series	Number of larvae per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
4104-91.54	3	13	5	26	41	9	0						97
4105-89.38	2	0	0	25	1	10	1		0				39
4105-92.39	3	9	0	16	21	18	0		0				67
4106-84.37N	0	0	0	0	5	6	8		1				20
4106-84.37D	0	0	0	0	6	25	15		0	0			46
4106-84.47N	0	0	0	2	28	10	1		0	0			41
4106-84.47D	0	0	0	0	15	27	16		7	0			65
4106-87.43D	0	0	0	0	0	1	0		0	0			1
5206-90.28N	0	0	23	22	3	0	0		0	0	0	0	48
5206-90.28D	0	0	1	30	2	0	0		0	0	0	0	33
5303-91.38N	1	0	9	71	62	76	5		1	0	0	0	225
5303-91.38D	0	9	7	16	7	7	0		0	0	0	0	46
5305-93.50N	60	24	12	22	6	0	0		0	0	0	0	124
5305-93.50D	0	2	48	24	52	18	0		0	0	0	0	144
5504-107.80	0	0	5	5	4	1	0	0	0	0			15
5504-110.60	2	0	2	1	32	3	0	0	0				40
5504-120.50	33	21	9	2	12	41	70	28	0	0	0		216
Total	104	78	121	262	297	262	116	28	9	0	0	0	1,267

numbers of larvae were taken within the zone of rapid temperature change (i.e., within the thermocline). In some series, however, the larvae occurred within a zone of uniform or nearly uniform temperature (series 5504-110.60 and 5303-91.38N). In series 5504-120.50, there were two levels of concentration of larvae, the upper occurring at 15.3° C., the lower at 12.2° C. There may have been two (or more) species of rockfish with different temperature requirements present in this series.

Rockfish are ovoviviparous; the eggs are carried by the female until embryonic development is completed. Hence, only the larvae are taken in plankton collections.

Sand Dabs (*Citharichthys* spp.)

Four species of *Citharichthys* occur off California and Baja California: *C. sordidus*, *C. stigmaeus*, *C. xanthostigma*, and *C. fragilis*. Larvae of all four species were taken in vertical distribution series. *C. sordidus* was taken in the series made off California, *C. xanthostigma* and *C. fragilis* in two series made off central Baja California, and *C. stigmaeus* in both areas. The larvae of these species will be described in a subsequent publication.

Citharichthys larvae were common in only 1 series, although they were taken in 14 (table 11). They occurred between the surface and approximately 88 meters (fig. 3, a). In Sebastian

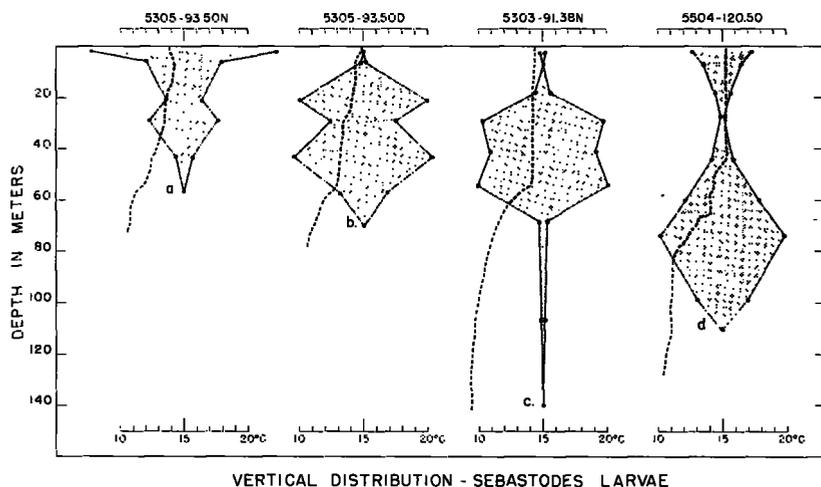


FIGURE 11.—Vertical distributions of *Sebastes* larvae in four separate series, with superimposed temperature profiles.

TABLE 11.—Depth distributions of the larvae of sand dabs (*Citharichthys spp.*)

Station series	Number per haul at average depth (m.) of—												Total
	2	8	19	28	41	56	72	88	105	138	215	285	
4104-91.54	1	0	0	2	4	0	0						7
4105-89.35	1	0	0	0	0	1	0						2
4105-92.39	0	1	4	2	1	0			0				8
4106-94.37D	0	0	0	0	1	1	0		0	0			2
4106-94.47N	0	0	0	0	1	2	0		0	0			3
4106-94.47D	0	0	0	0	2	1	0		0	0			3
4106-94.47N	0	0	0	0	0	1	0		0	0			1
4106-97.43N	1	0	0	0	0	0	0		0	0	0	0	1
5208-90.28N	0	2	1	2	31	66							102
5208-120.35	0	3	4	3	3	4	0		0	0	0	0	17
5303-91.38N	0	1	1	1	2	1	0		0	0	0	0	6
5303-91.38D	0	4	0	0	0	0	0		0	0	0	0	4
5305-93.50N	0	0	0	2	2	0	0		0	0	0	0	4
5305-93.50D	0	3	2	1	6	7	2	0	0	0	0	0	21
5504-120.50	0	3	2	1	6	7	2	0	0	0	0	0	21
Total	3	14	12	13	53	84	2	0	0	0	0	0	181

Viscaino Bay (5208-120.35), where the depth of the series was limited by the shallowness of the bay, most of the larvae were taken in the two deeper hauls.

Other Flatfish Larvae

Limited information on depth distributions of the larvae of four other species of flatfish is given in table 12. The distribution of *Symphurus atricauda* larvae at station 5208-120.35 is in contrast to the distribution of *Citharichthys* larvae at the same station. Most of the *Symphurus* larvae were taken in the upper haul of the series, and none was taken at the levels where most of the *Citharichthys* larvae occurred.

Lyopsetta exilis is close to the southern limit of its distribution in the series made off Point San Eugenio, Baja California (5504-120.50), hence it is not surprising that the larvae occurred only in the deeper hauls between 72 and 138 meters. In contrast to the relation noted between *Symphurus*

larvae and *Citharichthys* larvae in Sebastian Viscaino Bay, *Lyopsetta* larvae occurred almost completely below the level of occurrence of *Citharichthys* larvae at station 5504-120.50.

Lanternfish (Myctophid) Larvae

There is some information on the vertical distribution of 11 kinds of lanternfish (myctophid) larvae, although 3 species occurred in but a single series each. Four kinds were taken only in series made off southern California, three in series made off central Baja California, and four occurred in both areas. These distributions are consonant with the more detailed distributions obtained from the CCOFI cruises.

Larvae of *Diogenichthys laternatus* and *Lowena rara* have seldom been taken north of central Baja California; larvae of *Lampanyctus leucop-sarus* and *Tarletonbeania crenularis* are uncommon south of California. *Lampanyctus mexicanus* and *L. ritteri* are taken both off southern

TABLE 12.—Depth distributions of the larvae of other flatfish

Station series	Number per haul at average depth (m.) of—												Total
	2	8	19	28	41	56	72	88	105	138	215	285	
<i>Lyopsetta exilis</i> : 5504-120.50	0	0	0	0	0	0	3	3	2	2	0		10
<i>Paralichthys californicus</i> :													
4106-94.47D	0	0	0	0	1	0	0		0	0			1
5208-120.35	0	0	0	0	1	0							1
Total	0	0	0	0	2	0	0		0	0			2
<i>Pleuronichthys decurrens</i> :													
5303-91.38N	0	1	2	0	1	0	0		0	0	0	0	4
5303-91.38D	0	3	0	1	0	0	0		0	0	0	0	4
Total	0	4	2	1	1	0	0		0	0	0	0	8
<i>Symphurus atricauda</i> : 5208-120.35	30	6	1	2	0	0							39

TABLE 13.—Summary of depth distributions of lanternfish larvae, and their relation to temperature

	Number of series in which species occurred	Total number of individuals taken	Depth range (m.)	Depth of greatest abundance (m.)	Temperature range (° C.)	Weighted mean temperature (° C.)
<i>Lampanyctus leucopsarus</i>	15	619	8-105	28	9.7-16.1	13.2
<i>Lampanyctus mexicanus</i>	15	273	2-138	41	13.3-16.1	15.2
<i>Lampanyctus ritteri</i>	19	173	2-105	41	11.2-16.1	14.5
<i>Lampanyctus regalis</i>	1	1	56	56	-----	-----
<i>Diogenichthys atlanticus</i>	2	5	8-72	72	14.1-18.5	14.6
<i>Diogenichthys laternatus</i>	3	110	28-105	72	13.2-18.5	-----
<i>Electrona</i> spp.....	9	20	8-138	105	9.1-15.3	11.0
<i>Lowena rara</i>	1	3	41-56	56	16.5	16.5
<i>Myctophum californiense</i>	7	18	28-105	88	9.7-15.4	14.0
<i>Myctophum margaritatum</i>	1	2	88	88	14.3	14.3
<i>Tarletonbeania crenularis</i>	6	66	28-138	56	9.0-13.4	10.7

¹ Based on average depth (in meters) of the shallowest and deepest haul in which specimens occurred.

California and off central Baja California. However, *L. mexicanus* is near the northern limit of its distribution off southern California, while *L. ritteri* is near the southern limit of its distribution off central Baja California.

A summary tabulation of the depth distributions of lanternfish larvae is given in table 13. The temperature range over which each species was taken also is included, along with the weighted mean temperature of occurrence for each species. The occurrences in separate hauls are given for the larvae of *Lampanyctus leucopsarus* in table 14, of *L. mexicanus* in table 15, of *L. ritteri* in table 16, of *Tarletonbeania crenularis* in table 17, of *Diogenichthys laternatus* in table 18, and of the remaining kinds of lanternfish in table 19. The weighted average depth distributions of the five most common kinds of lanternfish larvae are illustrated in figure 12.

Only three species, all belonging to the genus *Lampanyctus*, were common in the vertical series.

Lampanyctus ritteri had the most widespread distribution of any kind of fish larvae, being taken in 19 of the 22 series. *L. leucopsarus* and *L. mexicanus* each occurred in 15 series.

A notable feature of the depth distributions of lanternfish larvae is their paucity above 23 meters. Six of the species were not taken in this stratum; *Electrona* spp. and *Diogenichthys atlanticus* each had one occurrence, and only about 5 percent (±6 percent) of the larvae of *Lampanyctus leucopsarus*, *L. mexicanus*, and *L. ritteri* were taken in this layer.

Lanternfish larvae occurred mostly in the upper mixed layer above the thermocline or in the upper part of the thermocline. The three common species of *Lampanyctus* appear to have the shallowest distributions: *L. leucopsarus* occurred in greatest abundance in the hauls averaging 28 meters deep, *L. mexicanus* and *L. ritteri* in the hauls averaging 41 meters deep. Less than 2 percent of the larvae of *L. leucopsarus* were found to occur

TABLE 14.—Depth distributions of the larvae of *Lampanyctus leucopsarus*

Station series	Number per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
4104-91.54.....	0	0	0	0	19	16	0	-----	-----	-----	-----	-----	35
4105-89.38.....	0	0	0	2	2	11	3	-----	-----	-----	-----	-----	18
4105-92.39.....	0	0	5	8	10	2	0	0	-----	-----	-----	-----	25
4106-94.37D.....	0	0	0	3	0	0	1	0	0	0	-----	-----	4
4106-94.47N.....	0	0	0	0	3	3	0	0	0	0	-----	-----	6
4106-94.47D.....	0	0	0	5	0	2	0	0	0	0	-----	-----	7
4106-97.43N.....	0	0	0	0	0	0	1	0	0	0	-----	-----	1
5206-90.28N.....	0	0	4	148	5	1	0	0	0	0	0	0	158
5206-90.28D.....	0	0	0	2	1	1	0	0	0	0	0	0	4
5303-91.38N.....	0	0	0	65	18	32	3	1	0	0	0	0	119
5303-91.38D.....	0	3	5	8	4	38	0	2	0	0	0	0	60
5305-93.50N.....	0	0	2	26	12	11	0	0	0	0	0	0	51
5305-93.50D.....	0	0	14	30	48	20	0	0	0	0	0	0	112
5403.94.80N.....	0	0	0	0	0	1	9	0	0	0	0	0	10
5403-94.80D.....	0	0	0	0	0	3	6	0	0	0	0	0	9
Total.....	0	3	30	297	122	141	23	-----	3	0	0	0	619

TABLE 15.—Depth distributions of the larvae of *Lampanyctus mexicanus*

Station series	Number per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
4104-89.38	0	0	0	0	1	0	0	0	0	0	0	0	1
4105-82.39	0	0	1	14	0	0	0	0	0	0	0	0	15
4106-84.37N	0	0	1	3	1	0	0	0	0	0	0	0	5
4106-84.37D	0	0	0	0	1	0	0	0	0	0	0	0	1
4106-84.47N	0	0	8	11	0	0	0	0	0	0	0	0	19
4106-84.47D	0	0	0	0	2	0	0	0	0	0	0	0	2
4106-87.43N	0	0	3	20	3	1	0	0	0	0	0	0	27
4106-87.43D	0	0	0	5	7	2	0	0	0	0	0	0	14
5206-80.28N	0	0	3	0	0	0	0	0	0	0	0	0	3
5305-83.50N	0	0	0	2	0	0	0	0	0	0	0	0	2
5403-84.80N	0	0	0	0	0	5	0	0	0	0	0	0	5
5504-107.80	0	0	0	0	21	36	21	9	0	1	0	0	88
5504-110.60	3	0	0	0	22	4	6	1	0	0	0	0	36
5504-120.50	2	3	2	3	5	7	0	0	0	0	0	0	22
5504-130.60	0	0	0	1	15	14	3	0	0	0	0	0	35
Total	5	3	18	59	78	69	30	10	0	1	0	0	273

TABLE 16.—Depth distributions of the larvae of *Lampanyctus ritteri*

Station series	Number per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
4104-81.54	0	0	0	0	5	0	0	0	0	0	0	0	5
4105-89.38	0	0	0	2	0	0	0	0	0	0	0	0	2
4105-82.39	0	0	2	15	2	0	0	0	0	0	0	0	19
4106-84.37N	0	0	0	0	1	0	0	0	0	0	0	0	1
4106-84.37D	0	0	0	0	2	0	0	0	0	0	0	0	2
4106-84.47N	0	0	0	0	1	0	0	0	0	0	0	0	1
4106-84.47D	0	0	0	1	2	0	0	0	0	0	0	0	4
4106-87.43N	0	0	0	0	5	1	0	0	0	0	0	0	6
4106-87.43D	0	0	1	0	0	0	0	0	0	0	0	0	1
5206-80.28N	0	0	1	1	0	0	0	0	0	0	0	0	2
5206-80.28D	0	0	0	5	0	4	0	0	0	0	0	0	9
5303-81.38N	0	0	1	0	2	2	0	0	0	0	0	0	5
5303-81.38D	0	0	0	10	0	0	0	0	0	0	0	0	10
5305-83.50N	0	0	0	0	4	0	0	0	0	0	0	0	4
5305-83.50D	0	1	0	0	0	9	9	0	0	0	0	0	19
5403-84.80N	0	0	2	3	5	10	1	0	0	0	0	0	21
5403-84.80D	0	0	0	3	9	9	8	8	1	0	0	0	38
5504-107.80	0	0	0	0	6	0	3	2	0	0	0	0	11
5504-110.60	1	1	0	0	1	5	5	0	0	0	0	0	13
5504-120.50	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	1	2	7	40	44	42	26	10	1	0	0	0	173

TABLE 17.—Depth distributions of the larvae of *Tarletonbeania crenularis*

Station series	Number per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
5206-80.28N	0	0	0	10	3	0	0	0	0	0	0	0	13
5206-80.28D	0	0	0	1	8	23	2	0	0	0	0	0	34
5303-81.38N	0	0	0	0	0	0	1	0	0	0	0	0	1
5303-81.38D	0	0	0	0	0	1	0	0	0	0	0	0	1
5305-83.50N	0	0	0	4	2	3	0	0	0	0	0	0	11
5305-83.50D	0	0	0	0	2	2	1	3	3	0	0	0	6
Total	0	0	0	15	13	29	4	4	4	1	0	0	66

TABLE 18.—Depth distributions of the larvae of *Diogenichthys laternatus*

Station series	Number per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
5504-107.80	0	0	0	0	0	0	0	0	1	0	0	0	1
5504-110.60	0	0	0	0	0	0	0	0	1	0	0	0	1
5504-130.60	0	0	0	1	2	2	64	36	3	0	0	0	108
Total	0	0	0	1	2	2	64	36	5	0	0	0	110

TABLE 19.—Depth distributions of the larvae of other myctophids

Station series	Number per haul at an average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
<i>Diogenichthys atlanticus:</i>													
4106-94.37N	0	1	0	0	0	0	0	0	0	0	0	0	1
5403-94.80N	0	0	0	0	0	1	3	0	0	0	0	0	4
Total	0	1	0	0	0	1	3	0	0	0	0	0	5
<i>Electrona</i> spp.:													
4104-91.54	0	0	0	0	0	0	0	0	1	0	0	0	1
4106-94.37N	0	0	0	0	0	0	1	5	1	0	0	0	2
4106-94.47N	0	0	0	0	0	1	2	0	2	0	0	0	5
5206-90.28N	0	0	0	0	0	1	0	0	0	0	0	0	1
5303-91.38N	0	0	0	0	0	0	1	0	0	0	0	0	1
5403-94.80N	0	0	0	0	0	0	0	0	3	1	0	0	4
5403-94.80D	0	0	0	0	0	0	0	0	1	0	0	0	1
5504-107.80	0	0	0	0	0	0	0	0	0	3	0	0	3
5504-120.50	0	1	0	0	0	0	0	1	0	0	0	0	2
Total	0	1	0	0	0	2	4	1	8	4	0	0	20
<i>Lampanyctus regalis:</i> 4106-97.43N	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Loweina rara:</i> 5504-130.60	0	0	0	0	1	2	0	0	0	0	0	0	3
<i>Myctophum californiense:</i>													
4105-92.39	0	0	0	2	0	0	0	0	0	0	0	0	2
4106-94.37D	0	0	0	0	0	0	0	0	1	0	0	0	1
4106-94.47N	0	0	0	0	2	0	0	0	0	0	0	0	2
4106-97.43N	0	0	0	0	0	2	0	0	0	0	0	0	2
5403-94.80N	0	0	0	0	0	1	0	0	0	0	0	0	1
5504-107.80	0	0	0	0	0	0	2	5	2	0	0	0	9
5504-120.50	0	0	0	0	0	1	0	0	0	0	0	0	1
Total	0	0	0	2	2	4	2	5	3	0	0	0	18
<i>Myctophum margaritatum:</i> 5504-107.80	0	0	0	0	0	0	0	2	0	0	0	0	2

below 88 meters. About 4 percent of the larvae of *L. mexicanus* and *L. ritteri* occurred below 88 meters.

Information on depth distributions of the eight other kinds of lanternfish larvae is suggestive, although fragmentary. Larvae of *Diogenichthys laternatus* were mostly taken in one series (108 larvae at 5504-130.60), hence our information on the depth distribution of this species is almost wholly confined to the distribution at a given place at a given time. In this situation, *D. laternatus* occurred at the bottom of the upper mixed layer. Although larvae of *Tarletonbeania crenularis*, *Myctophum californiense*, and *Electrona* spp. occurred in 6 or more series, the largest number of individuals of each that were taken in any one series was 34, 9, and 5, respectively. Despite the limited material, it is evident that the larvae of all three species have somewhat deeper vertical distributions than the larvae of *Lampanyctus*. *Electrona* spp. have the deepest distribution of any of the lanternfish larvae: about 60 percent of the larvae were taken at depths of 105 meters or below.

The temperatures at which the three common species of myctophid larvae were taken in the

vertical distribution studies reflect their geographical distribution. Larvae of the more northerly distributed *Lampanyctus leucopsarus* occurred at a mean temperature of 13.2° C., larvae of the intermediately distributed *L. ritteri* at a mean temperature of 14.5° C., and larvae of the more southerly *L. mexicanus* at a mean temperature of 15.2° C.

The mean temperatures of occurrence of larvae of *Tarletonbeania* and *Electrona* spp. were several degrees below that for the other lanternfish larvae; *Tarletonbeania* larvae occurred at a mean temperature of 10.7° C., *Electrona* larvae at 11.0° C. These temperatures are quite similar, yet the larvae of *Electrona* are taken considerably farther south than those of *Tarletonbeania*. This is made possible by the greater depth at which *Electrona* larvae occur.

There are not many stations at which it is possible to compare the depth distributions of different kinds of myctophid larvae. At most stations where species of *Lampanyctus* occurred together, their depth distributions were fairly similar. The distributions of *L. leucopsarus* and *Tarletonbeania crenularis* were similar in 5206-90.28N but *Tarletonbeania* larvae had a wider

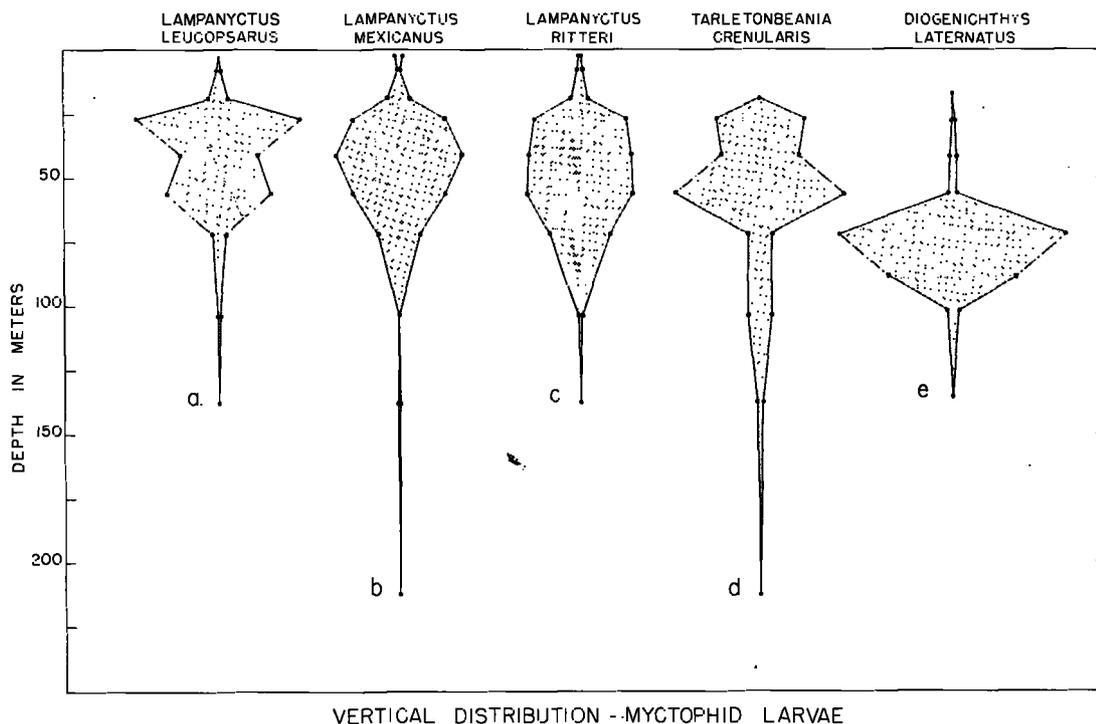


FIGURE 12.—Weighted average vertical distributions of the larvae of five species of myctophids.

depth range at station 5305–93.50N. There was a more marked contrast in the distributions of the larvae of *L. mexicanus* and *Diogenichthys laternatus* at station 5504–130.60: 29 of the 33 larvae of the former species occurred in the hauls averaging 41 and 56 meters deep, while 100 of the 108 larvae of *D. laternatus* were taken in the hauls averaging 72 and 88 meters. Hence, at this locality the larvae of these two species were fairly well separated in their depth distributions.

Leuroglossus stilbius

Larvae of *Leuroglossus stilbius* have the deepest distribution of any of the species studied. They have been taken in the bottom haul of a number of series, hence must occur at still deeper levels than those sampled in taking vertical distribution series. This is the only common species taken in vertical series for which it was found that the larger proportion of the larvae occurred below a depth of 100 meters.

Leuroglossus larvae were taken in 16 series, eggs in 5 (table 20). The weighted average vertical distribution of larvae is shown in figure 2, d. The depth of occurrence of larvae appears to be influenced by the depth of the thermocline. The

shallowest thermocline encountered while taking vertical series was at station 5206–90.28 N, and here the larvae occurred nearer to the surface than in other series. At several stations where both day and night series were taken, the larvae had a somewhat shallower distribution in the night series.

The vertical distributions of eggs and larvae of *Leuroglossus* are illustrated in figure 13. The depth range of eggs and larvae is fairly similar at station 5504–120.50 (fig. 13, b and e). Except for a few larvae at the surface, no eggs or larvae were taken in the upper six hauls, and both eggs and larvae were taken in the five lower hauls. Abundance within the zone of occurrence differed for the two categories: the largest number of eggs occurred in the haul averaging 110 meters deep; the largest number of larvae was obtained in the haul averaging 137 meters deep.

Both eggs and larvae were exceedingly abundant at station 5303–91.38. Over three times as many eggs were taken in the night series as in the day, possibly indicating a difference in the water mass being sampled during the two periods. In the night series most eggs were taken between the surface and 88 meters (fig. 13, c), with a marked

TABLE 20.—Depth distributions of the larvae and eggs of *Leuroglossus stilbius*

Station series	Number per haul at average depth (m.) of—												Total
	2	8	19	28	41	56	72	88	105	138	215	285	
Larvae:													
4104-91.54	0	0	0	0	0	9	9						18
4105-92.39	0	0	0	0	3	59	5		3				70
4106-94.37N	0	0	0	0	1	0	0		1				2
4106-94.37D	0	0	0	0	0	0	1		0	0			1
4106-94.47N	0	0	0	0	1	4	9		1	2			22
4106-94.47D	0	0	0	0	0	0	0		0	0			1
4106-97.43N	0	0	0	0	0	0	1		0	0			1
5206-90.28N	3	0	0	22	10	4	4		5	5	6	1	60
5206-90.28D	0	0	0	0	1	8	14		1	1			30
5303-91.38N	0	0	1	0	0	104	260		11	6	57	21	460
5303-91.38D	0	0	0	0	6	0	10		32	23	3		74
5305-93.50N	0	0	0	2	0	11	2		10	0	0	0	25
5305-93.50D	0	0	0	0	0	0	3		4	0	0		7
5403-94.80D	0	0	0	0	0	0	0		0	1	0		1
5504-110.60	3	0	0	0	0	0	0		2				5
5504-120.50	4	0	0	0	0	0	9		11	12	19	6	61
Total	10	0	1	25	25	204	324	11	85	57	72	24	838
Eggs:													
5303-91.38N	102	91	270	1,160	981	7,428	2,873		46	0	38	39	13,028
5303-91.38D	305	311	271	516	640	696	232		1,175	3	4		4,158
5403-94.80D	0	0	0	0	0	1	5		0	1	0		7
5504-120.50	6	0	0	0	0	0	26		115	160	54	1	362
Total	413	402	541	1,676	1,621	8,125	3,136	115	1,381	63	43	39	17,555

concentration at approximately 54 meters (7,428 eggs in this one haul). The eggs in the day series were mostly taken between the surface and 122 meters (fig. 13, d), with the largest concentration at 92 meters. Larvae were about six times as abundant in the night series as in the day. In the night series most larvae occurred in the hauls made between 54 and 291 meters, with the largest concentration at approximately 68 meters (fig. 13, a). Most larvae in the day series occurred in contiguous hauls with average depths of 92 and 139 meters.

The lower limit of the temperature of occurrence of *Leuroglossus* larvae in vertical series is not known, since temperature observations were not available for some of the deeper hauls.

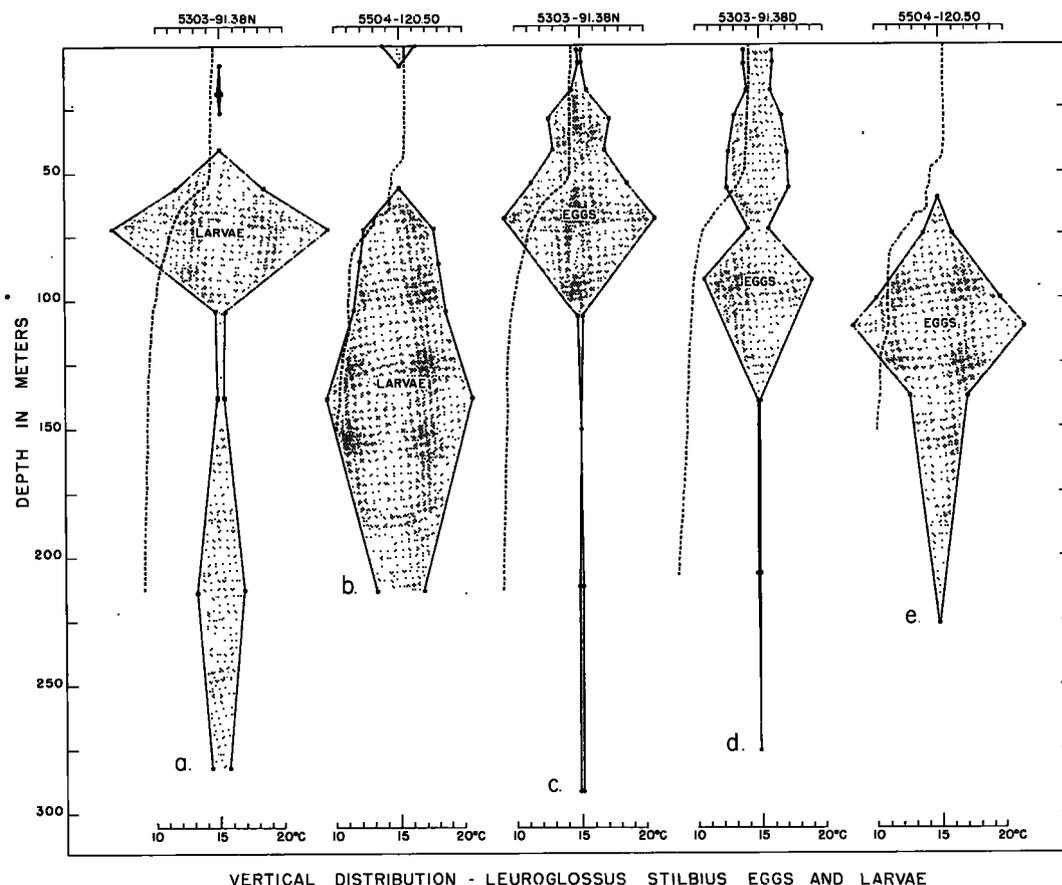
Larvae were taken at temperatures at least as low as 8.6° C. Nearly half of the occurrences were at temperatures below 10° C., and barely a fourth of the occurrences were at temperatures above 12° C. The overall temperature range for larvae was 8.6° to 16.6° C. The temperature range for eggs was from 8.6° to 15.3° C., with more occurrences at temperatures above 12° C. than below.

Bathylagus wesethi

Originally described from off Monterey, the type locality has since proved to be near the northern limit of the range of this species. The larvae are widely distributed off southern California and Baja California. The larvae of this species were taken in six series, the eggs in six (table 21).

TABLE 21.—Depth distributions of the larvae and eggs of *Bathylagus wesethi*

Station series	Number per haul at average depth (m.) of—												Total
	2	8	19	28	41	56	72	88	105	138	215	285	
Larvae:													
5305-93.50D	0	0	0	0	0	0	0		1	0	0		1
5402-94.80N	0	0	0	0	0	0	2		0	0	0		2
5402-94.80D	0	0	0	0	0	5	0		0	0	0		5
5504-107.80	1	0	0	0	0	0	2		38	20	5		66
5504-110.60	0	0	0	0	0	2	0		1	1			4
5504-120.50	0	0	0	0	1	1	4		0	0	0		6
Total	1	0	0	0	1	8	8	39	22	5	0		84
Eggs:													
5402-94.80N	0	1	0	0	0	12	45		1	1	1		61
5402-94.80D	0	0	0	0	4	8	8		0	0	0		20
5504-107.80	1	1	0	0	0	1	2		8	12	1		26
5504-110.60	1	0	1	0	1	5	12		31	41			92
5504-120.50	1	2	2	0	0	0	2		1	0	0		8
5504-130.60	0	0	0	0	0	1	2		0	0	0		3
Total	3	4	3	0	5	27	71	40	54	2	1		210



VERTICAL DISTRIBUTION - LEUROGLOSSUS STILBIUS EGGS AND LARVAE

FIGURE 13.—Vertical distributions of *Leuroglossus stilbius* larvae and eggs in separate series, with superimposed temperature profiles.

The only series in which larvae were at all common was 5504-107.80. Except for one larva in the surface haul, all larvae occurred in the four lower hauls, having average depths of 70, 88, 111, and 142 meters, and the greatest numbers of larvae were taken in the two middle hauls of this group.

Of the 84 larvae collected in all series, only 2 were taken in the upper 50 meters (table 4). A smaller proportion of the larvae of *Bathylagus wesethi* than of *Leuroglossus stilbius* were taken in the deeper hauls, and there is no clear-cut evidence that larvae of *B. wesethi* occurred below the levels sampled.

Eggs of *B. wesethi* were rather common in two series (5403-94.80N and 5504-110.60). In the former series, most eggs occurred between 50 and 100 meters deep (fig. 5, e), in the latter series, which extended only to approximately 105 meters the largest numbers were taken in the bottom haul.

Other Deep-Sea Smelts

Larvae of five additional species of deep-sea smelts were taken in the vertical series (table 22), but only one species occurred in even moderate abundance. Most occurrences were within or below the thermocline.

An undescribed species of *Bathylagus* was taken in 13 series, mostly less than 5 individuals per series. Most of these larvae were obtained between 50 and 100 meters deep. This species is more northerly in its distribution than *Bathylagus wesethi*, and the occurrences off central Baja California are near the southern limit of its distribution.

The *Nansenia* sp. is also probably undescribed. There are two or three species of this genus in the eastern North Pacific, none of which has been previously reported.

TABLE 22.—Depth distributions of the larvae of other deep-sea smelts

Station series	Number per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
<i>Argentina sialis:</i>													
5206-90.28N	0	0	0	1	0	0	0	0	0	0	0	0	1
5504-120.50	0	0	0	0	0	0	0	0	1	2	0	0	3
Total	0	0	0	1	0	0	0	0	1	2	0	0	4
<i>Bathylagus alascanus:</i> 5403-94.80N													
	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Bathylagus</i> sp.:													
4104-91.54	0	0	0	0	0	3	2	0	0	0	0	0	5
4105-92.39	0	0	0	0	0	14	0	0	0	0	0	0	14
4106-94.37N	0	0	0	0	0	0	1	0	1	0	0	0	2
4106-94.37D	0	0	0	0	0	0	0	0	1	0	0	0	1
4106-94.47N	0	0	2	1	0	2	1	0	0	0	0	0	6
4106-94.47D	0	0	0	0	0	0	2	0	0	0	0	0	2
4106-97.43N	0	0	0	0	0	1	0	0	0	0	0	0	1
5206-90.28N	1	0	0	1	0	0	0	0	0	0	0	1	3
5303-91.38N	0	0	0	2	0	0	6	0	0	0	0	0	8
5303-91.38D	0	0	0	0	1	0	0	0	0	0	0	0	1
5305-93.50N	0	0	0	0	0	2	0	0	0	0	0	0	2
5504-107.80	0	0	0	0	0	0	0	0	0	1	0	0	1
5504-120.50	0	0	0	0	0	0	1	0	0	0	0	0	1
Total	1	0	2	4	1	22	13	0	2	1	0	1	47
<i>Microstoma</i> sp.:													
5206-90.28N	0	0	0	0	0	1	0	0	0	0	0	0	1
5206-90.28D	0	0	0	0	0	0	1	0	0	0	0	0	1
5403-94.80N	0	0	0	0	0	0	0	0	3	0	0	0	3
Total	0	0	0	0	0	1	1	0	3	0	0	0	5
<i>Nansenia</i> sp.: 5504-107.80													
	0	0	0	0	0	0	0	0	0	2	0	0	2

Vinciguerria lucetia

The eggs and larvae of this species are not as well represented in vertical series as would be anticipated from their abundance in the CCOFI area (table 23). The weighted average vertical distribution of larvae is shown in figure 2, c. The only series in which the larvae were common was 5504-130.60. The thermocline was deep at this station, as was evident from bathythermograms made at the station. These records were subsequently lost. The larvae were distributed in the upper mixed layer (0-80 meters). *Vinciguerria* eggs had a wider depth distribution at this station than the larvae (5 to 121 meters; fig. 5, d).

Eggs occurred in all hauls of the shallow series, 5504-110.60, the deepest haul of which averaged 105 meters.

Other Larvae

Limited information on the vertical distribution of 16 kinds of larvae is given in table 24. Larvae of *Chromis punctipinnis* (blacksmith) and of *Sphyræna argentea* (barracuda), each taken in three series, occurred only in the two shallowest hauls. The larvae of another commercially important species, *Palometa simillima* (pompano), occurred between the surface and 48 meters deep.

TABLE 23.—Depth distributions of the larvae and eggs of *Vinciguerria lucetia*

Station series	Number per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
Larvae:													
4106-97.43N	1	0	0	0	0	0	0	0	0	0	0	0	1
5504-107.80	0	0	0	0	2	2	8	4	0	0	0	0	16
5504-110.60	0	0	0	0	0	2	11	9	3	0	0	0	25
5504-120.50	4	1	0	0	0	0	0	0	0	0	0	0	5
5504-130.60	2	0	29	33	41	6	1	0	0	0	0	0	112
Total	7	1	29	33	43	10	20	13	3	0	0	0	159
Eggs:													
5504-107.80	0	0	0	0	0	0	0	0	4	2	0	0	6
5504-110.60	3	9	12	1	13	8	4	11	14	0	0	0	75
5504-130.60	0	4	4	12	15	15	13	10	1	0	0	0	74
Total	3	13	16	13	28	23	17	21	19	2	0	0	155

TABLE 24.—Depth distributions of other larvae taken in vertical distribution series—Continued

Station series	Number per haul at average depth (m.) of—											Total	
	2	8	19	28	41	56	72	88	105	138	215		285
<i>Trachypterus rezsalmorum:</i>													
5403-94.80N	0	0	0	0	0	1	0	0	0	0	0	0	1
5403-94.80D	1	0	0	0	0	0	0	0	0	0	0	0	1
Total	1	0	0	0	0	1	0	0	0	0	0	0	2
Labrids:													
4105-89.38	0	2	0	2	0	0	0	0	0	0	0	0	4
4105-92.39	6	2	0	0	0	0	0	0	0	0	0	0	8
4106-94.47N	0	1	0	1	0	0	0	0	0	0	0	0	2
4106-94.47D	7	3	1	0	0	0	0	0	0	0	0	0	11
5206-90.28N	26	25	6	0	0	0	0	0	0	0	0	0	57
5206-90.28D	1	0	0	0	0	0	0	0	0	0	0	0	1
5303-91.38N	0	0	1	0	0	0	0	0	0	0	0	0	1
5305-93.50D	0	0	2	0	2	0	0	0	0	0	0	0	4
5504-120.50	0	0	0	0	0	1	0	0	0	0	0	0	1
Total	40	33	10	3	2	1	0	0	0	0	0	0	89

Two species have been included under labrids: *Halichoeres semicinotus* and *Oxyjulis californica*. There is such a marked difference in the abundance of labrid larvae in the replicate series taken at station 5206-90.28 (57 in night series, 1 in day series) that this must reflect rather marked horizontal clumping of the larvae associated with a change in the water mass between the night and day series. More than 90 percent of the labrid larvae occurred above 23 meters.

The few larvae of *Chauliodus macouni* and *Idiacanthus antrostomus* were taken in hauls below 100 meters. A comparison based on closing and upper net hauls on Norpac confirms the deep distribution of the larvae of these two species. The few larvae of *Argyropelecus* spp. taken in these vertical series confirm the deep distribution of this category that is so strikingly shown in Norpac material (discussed in a following section).

Larvae of *Cyclothone* spp. appear to have a distribution similar to that of *Vinciguerria lucetia*. Larvae of *Melamphaes* spp. (mostly *M. lugubris* and *M. bispinosus*) appear to occur mostly within or below the thermocline.

Discussion

The two most striking facts brought out by the present studies on vertical distribution of fish eggs and larvae are the following:

1. Most fish eggs and larvae occur within the upper mixed layer or in the upper portion of the thermocline—between the surface and approximately 125 meters. Of the 15 most common kinds

of larvae taken in vertical distribution studies, 12 were so distributed.

2. Within this zone of occurrence, all of the more common kinds of fish eggs and larvae showed marked differences in vertical distribution from series to series.

In the light of these findings on vertical distribution of fish eggs and larvae, it appears to me that the best method for quantitatively sampling this parameter is by oblique net hauls taken between the surface and at least 125 meters. It is impossible to obtain a representative sampling of fish eggs and larvae by sampling at any one level, such as a horizontal surface tow. In the four series where sardine eggs were common, from 15 to 85 percent of the total number were taken in surface hauls. Similarly, from 0 to 60 percent of sardine larvae were taken in surface hauls, 0 to 35 percent of anchovy larvae, 2 to 50 percent of jack mackerel larvae, 0 to 50 percent of rockfish larvae, and so on.

VERTICAL DISTRIBUTION DATA FROM NORPAC SAMPLES

Norpac is the name given to the most extensive simultaneous coverage of an oceanic area that has yet been made. In July to September 1955, a systematic coverage of the North Pacific Ocean, north of 20° N. latitude, was carried out cooperatively by research groups in the United States, Canada, and Japan. The section of Norpac that was occupied by agencies participating in the California Cooperative Oceanic Fisheries Investigations extended from Cape San Lucas,

Baja California, to the Straits of Juan de Fuca, and offshore to 150° W. longitude. The following discussion is based solely on material collected in the CCOFI section of Norpac.

Two net hauls were taken simultaneously at the majority of stations occupied on Norpac (139 stations). A closing net was fastened to the towing cable 200 meters below a standard open plankton net. The closing net was opened immediately before attachment of the upper net and closed immediately after retrieving the upper net at the completion of a tow. The upper net was lowered on 200 additional meters of cable and then hauled obliquely upward. The actual stratum fished by the upper net differed from station to station, depending on variations in vessel speed, state of the sea, et cetera, but averaged 131 meters to the surface. The range in depths fished by the upper net at different stations was from 88 to 146 meters. The closing net fished from depths of approximately 262 meters to 131 meters on the average, but on occasion was as shallow as 88 meters.

A comparison of the larvae taken in the two hauls on stations where both nets were used is given in table 25. Only those categories are in-

TABLE 25.—Comparison of number of larvae taken in upper net and closing net hauls at stations occupied on Norpac, August–September, 1955

	Upper net hauls ¹	Closing net hauls ²	Total both levels	Percentage of total taken in closing-net hauls
Total (139 hauls).....	6,358	705	7,063	10
<i>Sardinops caerulea</i>	8	0	8	0
<i>Engraulis mordax</i>	99	1	100	1
<i>Trachurus symmetricus</i>	22	0	22	0
<i>Sebastes</i> spp.....	35	1	36	3
<i>Citharichthys</i> spp.....	68	0	68	0
<i>Lampanyctus leucopsarus</i>	78	1	79	1
<i>Lampanyctus mexicanus</i>	483	1	484	1
<i>Lampanyctus ritleri</i>	72	6	78	8
<i>Lampanyctus regalis</i>	18	0	18	0
<i>Tarletonbeania crenularis</i>	42	11	53	21
<i>Diogenichthys atlanticus</i>	140	24	164	15
<i>Diogenichthys laternatus</i>	203	6	209	3
<i>Loneina rara</i>	10	7	17	41
<i>Myctophum californiense</i>	76	8	84	10
<i>Myctophum margaritatum</i>	25	2	27	7
<i>Electrona</i> spp.....	51	47	98	48
<i>Argentiniis</i>	53	32	85	39
<i>Vinciguerria</i> spp.....	1,605	30	1,635	2
<i>Cyclothone</i> spp.....	618	3	618	1
<i>Argyropelecus</i> spp.....	21	352	373	94
<i>Idiacanthus antrostromus</i>	58	25	83	32
<i>Chauliodon macouni</i>	5	13	18	72
<i>Melamphaes</i> spp.....	91	15	106	14
<i>Ichthyosoma lockingtoni</i>	5	2	7	29
<i>Trachipterus</i> spp.....	5	1	6	11
<i>Chromis punctipinnis</i>	10	0	10	0
All others.....	2,457	117	2,574	5

¹ Depth of upper-net hauls approximately 131–0 meters.

² Depth of closing-net hauls approximately 262–131 meters.

³ Includes *Leuroglossus stilbius*, *Bathylagus wesethi* and all other deep-sea smelts taken on Norpac.

cluded which are discussed in the preceding sections. About one-ninth as many larvae were taken in the closing net hauls as in the upper net hauls.

The information from these closing-net hauls is an interesting supplement to that given in the earlier portion of the paper. Actually both strata sampled on Norpac, 0 to 131 meters and 131 to 262 meters, were also covered in taking many of the vertical distribution series. The data from Norpac were much more extensive, however; hauls were taken at 139 stations on Norpac, as compared to the 22 vertical distribution series. The number of larvae per station was markedly fewer on Norpac: only 7,063 larvae were obtained in the combined haul data on Norpac, while 18,045 larvae were taken in vertical distribution series. Numbers are greater in the vertical distribution series, both because larval-rich areas were selected and considerably larger volumes of water were strained at each station. In fact, as much water was strained in taking each haul in a vertical series as was strained in a single net haul on Norpac.

Many of the categories discussed in the earlier sections of the paper are poorly represented in Norpac material. This is especially true of the categories that are routinely reported in the series, Sardine Eggs and Larvae and Other Fish Larvae, Pacific Coast (Ahlstrom and Kramer, 1957, Ahlstrom, 1958). Larvae of hake and Pacific mackerel were not taken at all, larvae of sardine, jack mackerel, and *Sebastes* spp. were rare, and only anchovy larvae occurred in even moderate abundance (100 individuals). The vertical distributions of these larvae in Norpac material, however, were similar to their distributions in the vertical series—only 0 to 3 percent were taken in the deeper closing-net hauls.

The most abundant category in the Norpac material was *Vinciguerria* spp. Three species are grouped in this category: *V. lucetia*, *V. nimbaria*, and *V. poweriae*, listed in order of their abundance. The presence of only 2 percent of the specimens in the deeper net supports the depth distribution of *Vinciguerria* larvae as determined from the less extensive material obtained in vertical distribution series.

Half of the larvae taken in closing-net hauls on Norpac belonged to a single genus, *Argyropelecus*. Larvae of this genus are seldom taken

in regular survey net tows, and the reason for this is apparent from Norpac results. Only 21 larvae were taken in upper-net hauls, while 352 occurred in hauls taken with the deeper-fishing closing net.

Seven other categories of larvae had 20 percent or more of their numbers in the closing-net hauls: argentinids, *Idiacanthus antrostomus*, *Chauliodus macroni*, *Ichthyos lockingtoni*, *Tarletonbeania crenularis*, *Loweina rara*, and *Electrona* spp. So few specimens of *Leuroglossus stilbius* and *Bathylagus wesethi* were taken on Norpac that all larvae of deep-sea smelts are grouped together as argentinids; about 40 percent of the specimens of argentinids were taken in the deep closing-net hauls. Information on depth distribution of *Idiacanthus antrostomus* is more complete from Norpac samples than from the vertical distribution series; about one-third of the specimens were taken in the deeper net on Norpac. Information on depth distribution of *Ichthyos lockingtoni* is meager in both sets of data; the presence of two specimens out of seven in the closing-net hauls on Norpac indicates a somewhat deeper distribution than was noted from vertical distribution series. Larvae of *Chauliodus* were more common in the closing-net hauls on Norpac than in the upper net hauls: 13 of the 18 larvae were from the deeper samples.

All 11 categories of myctophid larvae that were taken in vertical distribution series were also obtained in Norpac material. It is interesting to compare the depth distributions of the more common kinds, as determined from the two sets of data (table 26).

Larvae of *Lampanyctus leucopsarus* and *L. mexicanus* were almost entirely confined to upper net hauls on Norpac. These two species had the shallowest depth distributions of any lanternfish

larvae taken in vertical distribution series. Somewhat more larvae of *L. ritteri* were taken in closing net hauls on Norpac (8 percent of the total) than was indicated for these levels in vertical series. It will be recalled that the distribution of *Diogenichthys laternatus* in vertical series was based mostly on a single series. Larvae of this species were taken at a number of stations on Norpac. Only about 3 percent of the total occurred in the level fished by the closing net. Larvae of *Electrona* spp., which had the deepest distribution of any lanternfish in vertical series, also had the highest percentage occurrence in closing-net hauls on Norpac. A larger percentage of larvae of *Tarletonbeania crenularis* was taken in closing-net hauls on Norpac than in deeper levels in vertical distribution series.

UNDERSAMPLING OF FISH LARVAE DURING DAYTIME

Silliman (1943) called attention to undersampling of sardine larvae during daylight hours, based on data from the replicate vertical series taken at station 4106-94.37 and 4106-94.47. Ahlstrom (1954) gave data on the extent of undersampling of sardine larvae of different sizes in daylight hauls, based on 626 collections of sardine larvae. The statistics of a linear regression line fitted to the data show an increase in the ratio of larvae in night hauls to day hauls of 0.7 for each millimeter increase in size above 4.75 millimeters ($s_{yx}=0.96$). Thus, the number of 9.75-millimeter larvae in night hauls was five times as many as in day hauls, and the number of 15.75-millimeter larvae was nearly nine times as many.

A similar analysis has been made for catches of anchovy larvae. The night/day (N/D) ratio was found to increase 0.64 for each millimeter increase

TABLE 26.—Comparison of depth distributions of lanternfish larvae in Norpac material and vertical distribution series

	Norpac				Vertical distribution series		
	Number of larvae taken by—			Percentage in deeper haul (262-131 m.)	Total larvae obtained	Number of larvae taken below 100 m.	Percentage of total taken below 100 m.
	Upper net (131-0 m.)	Closing net (262-131 m.)	Both nets				
<i>Lampanyctus leucopsarus</i>	78	1	79	1	619	3	1
<i>Lampanyctus mexicanus</i>	483	1	484	0.2	273	1	1
<i>Lampanyctus ritteri</i>	72	6	78	8	173	1	1
<i>Diogenichthys laternatus</i>	203	6	209	3	110	5	5
<i>Tarletonbeania crenularis</i>	42	11	53	21	66	5	8
<i>Myctophum californiense</i>	76	8	84	10	18	3	17
<i>Electrona</i> spp.....	51	47	98	48	20	12	60

TABLE 27.—Diurnal differences in number of larvae taken in 63 replicate hauls at station 70.130, October 1950

	Total all hauls	Day hauls ¹		Night hauls		Ratio N/D
		Occurrences	Average per haul	Occurrences	Average per haul	
Total larvae.....	7,223		49.6		177.6	3.6
<i>Vinciguerria lucetia</i>	660	14	2.35	31	18.30	7.8
<i>Cyclohone</i> spp.....	850	14	2.10	32	24.52	11.7
<i>Bathylagus wesgthi</i>	2,139	31	23.10	32	44.58	1.9
<i>Ceratocopus townsendi</i>	955	16	2.60	32	27.30	10.5
<i>Diafus theta</i>	338	7	.90	31	9.75	10.8
<i>Digenichthys atlanticus</i>	183	7	.72	22	4.95	6.9
<i>Electrona</i> spp.....	252	10	1.28	28	6.68	5.2
<i>Lampanyctus ritteri</i>	173	3	.35	25	5.05	14.4
<i>Mycophum californiense</i>	379	13	2.18	28	9.70	4.4
<i>Idiacanthus antrostomus</i>	605	16	3.32	31	15.62	4.7
<i>Melamphaes</i> spp.....	146	11	1.68	19	2.90	1.7
<i>Brama brama</i>	136	12	1.20	19	3.05	2.5

¹ Based on 31 samples. One sample taken during daylight hours spoiled because preservative was not added.

in size above 3.5 millimeters. Thus, undersampling of larger larvae of anchovies during daytime is in the same order of magnitude as undersampling of sardine larvae.

Surprisingly enough, no consistent difference was found between the numbers of jack mackerel larvae in night and day hauls. The night/day ratio is close to 1. The analysis was based on nearly 1,000 samples containing jack mackerel larvae.

When data of larvae of other fishes are analyzed for night and day differences, most kinds are found to occur in markedly lower numbers in daytime hauls than in night hauls. The problem may be illustrated from data obtained on a special cruise made during October 1950. Three vessels participated in this cruise (cruise 5010), each holding a fixed geographical position on line 70 (off Monterey) while taking observations at 3-hour intervals over an 8-day period. The data

from station 70.130 (33°33' N. lat., 127°16.5' W. long.) have been summarized in table 27.

The total number of larvae taken in 32 night hauls at station 70.130 was 5,684, or an average of 177.6 larvae per haul; the number taken in 31 day hauls was 1,539, or an average of 49.6 larvae per haul. The night/day ratio for all larvae was 3.6. Twenty-eight kinds of larvae were taken in the hauls, 12 kinds in some abundance. The night/day ratios for the latter were all larger than one. The lowest ratio was 1.7 for *Melamphaes* spp., the highest 14.4 for *Lampanyctus ritteri*.

REPLICATE VERTICAL DISTRIBUTION SERIES

In order to obtain information on differences in vertical distribution of larvae during day and night, and also on daytime undersampling of larvae, replicate vertical series were taken at seven localities. The data are summarized in table 28.

TABLE 28.—Night vs. daytime sampling of larvae in 7 replicate vertical distribution series [N=night series; D=day series]

Species	Number of larvae taken at station—																Ratio N/D
	4106-94.37		4106-94.47		4106-97.43		5206-90.28		5303-91.38		5305-93.50		5403-94.80		Total		
	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	
<i>Sardinops caerulea</i>	40	6	89	24	1	0	5	3	0	0	0	0	10	4	145	37	3.9
<i>Engraulis mordax</i>	27	4	217	10	12	0	612	151	12	0	10	20	0	0	890	185	4.8
<i>Trachurus symmetricus</i>	0	1	7	0	0	0	26	2	0	0	4	2	52	210	89	215	0.4
<i>Sebastes</i> spp.....	20	46	41	65	0	1	48	33	225	46	124	144	0	0	458	335	1.4
<i>Merluccius productus</i>	3	0	8	0	1	0	0	0	20	5	0	0	1,753	707	1,785	712	2.5
<i>Leuroglossus stilbius</i>	2	1	22	1	1	0	60	30	460	74	25	7	0	1	570	114	5.0
<i>Lampanyctus leucoparus</i>	0	4	6	7	1	0	158	4	119	60	51	112	10	9	345	196	1.8
<i>Lampanyctus mexicanus</i>	5	1	19	2	27	14	3	0	0	0	0	5	0	61	17	3.6	
<i>Lampanyctus ritteri</i>	1	2	1	0	4	6	1	2	9	5	10	4	19	21	45	40	1.1
All others.....	5	5	34	23	6	2	110	56	83	18	19	34	26	14	283	152	1.9
Total.....	103	70	444	132	53	23	1,023	281	928	206	245	323	1,875	966	4,671	2,003	2.3

In all but one replicate series, more larvae were taken in night hauls than in daytime hauls. The night/day ratios for total larvae in the seven stations were as follows:

Station	Total larvae take in—		N/D ratio
	Night series	Day series	
4106-94.37	103	70	1.5
4106-94.47	444	132	3.4
4106-97.43	53	23	2.3
5206-90.28	1,023	281	3.5
5303-91.38	928	208	4.5
5305-93.50	245	323	0.8
5403-94.80	1,875	966	1.9
Total	4,671	2,008	2.3

Replicate series have several limitations that should be kept in mind. For one thing, it is almost impossible to sample the same water mass for a 24-hour period. If a geographical position is maintained, the water mass will change, slowly in some localities, rather rapidly in others, depending on the currents. Furthermore, water masses will move past the geographical position at different rates of speed at different levels. If an attempt is made to stay with a water mass, the investigator is still faced with the problem of water moving at different rates of speed at different levels. Furthermore, if larvae are sharply stratified in depth, the center of abundance may be missed on one, or both, of the series taken at a station. Any horizontal clumping of larvae will also affect the numbers taken in the two series.

There are some marked changes in abundance in the replicate series that must be due either to changes in water mass or to marked stratification or clumping of larvae. Two examples of marked stratification or clumping are the catch of 148 *Lampanyctus leucopsarus* larvae in the 27-meter haul at 5206-90.28N, and the catch of 1,622 hake larvae in the haul averaging 64 meters deep at 5403-94.80N. Two differences which appear to be due to a change in water mass are the marked

change in abundance of anchovy larvae at station 4106-94.47, decreasing from 217 larvae in the night series to only 10 in the day, and the daytime increase in abundance of jack mackerel larvae at station 5403-94.80 (210 larvae in day series, 52 in night).

It is interesting to note that only one kind of larva, jack mackerel, occurred in greater abundance in day hauls than in night. As pointed out earlier, this species has shown no consistent difference in abundance of larvae between day and night hauls on regular survey cruises. There is an inconsistency in the N/D ratio of *Lampanyctus ritteri* as obtained from replicate vertical series and from repeated sampling at station 5010-70.130. In the replicate series the ratio was only 1.1, but at station 70.130 the difference in abundance between night and day hauls was more marked than for any other species (N/D ratio 14.4). Individual species are treated in more detail in following sections.

Fish eggs should be taken in comparable abundance in both night and day hauls. Eggs can neither migrate vertically nor avoid the net. Hence any differences found in abundance of eggs in day and night hauls must be due to vertical stratification or horizontal clumping. The abundance of eggs in three replicate series is summarized in table 29. In two instances considerably more eggs were taken in the day series, in three instances more eggs were taken in the night series, and in one comparison the numbers were about equal in the two series. Some of the differences are quite large. Only 3 anchovy eggs were taken in the night series at station 5206-90.28, but 69 were taken in the day series. At station 5303-91.38, *Leuroglossus* eggs were more than three times as abundant in night hauls as in day hauls. A part of this difference is probably due to vertical stratification of the eggs, since 57 percent of the eggs in the night series were taken at one

TABLE 29.—Fish eggs taken in replicate vertical distribution series, by station and species

	Station 5206-90.28		Station 5305-91.38	Station 5403-94.80			
	<i>Sardinops caerulea</i>	<i>Engraulis mordax</i>	<i>Leuroglossus stibius</i>	<i>Sardinops caerulea</i>	<i>Trachurus symmetricus</i>	<i>Merluccius productus</i>	<i>Bathylagus wesethi</i>
Night series	6	3	13,028	271	1,117	102	61
Day series	3	69	4,158	201	2,196	101	20
Total	9	72	17,186	472	3,313	203	81

depth. A comparison of sardine eggs at station 5403-94.80 is given in the following section.

Sardine Larvae

Sardine larvae were not particularly abundant in the replicate hauls. The two best series were 4106-94.37 and 4106-94.47 (table 5): in the former, 40 larvae were taken in the night series, 6 in the day; in the latter, 89 in the night series, 24 in the day. Silliman (1943) has discussed these particular replicate series as they apply to the sardine larvae.

In night series, no sardine larvae were taken below 48 meters, while in day series five larvae occurred below this level. Sardine larvae taken in replicate series are grouped by size in table 30. A summary follows:

Size category (mm.)	Night series	Day series	N/D ratio
2.76-6.25	31	21	1.5
6.26-11.25	51	4	12.8
11.26-16.25	61	7	8.7
16.26 and larger	2	5	.4
Total	145	37	3.9

Although more of the larger sizes of sardine larvae were taken in night hauls than day, there is a discrepancy in the largest size category. More larvae of the largest category (16.26 mm. and larger) were taken in day hauls than night. Since this finding does not agree with the much larger mass of data available from routine hauls, it must be regarded as an artifact. It points up the variability that is encountered in individual situations, and the need for caution in interpreting data based on a limited number of observations. Interestingly enough, the five larvae taken below 48

meters in day hauls were all larger than 16.26 millimeters. These larvae occurred in hauls averaging 58, 60, and 73 meters deep. Since no larvae were taken below 48 meters in night hauls, it is assumed that there was a movement of larger larvae to deeper levels in the daytime.

Sardine Eggs

A comparison of sardine eggs in the replicate series at station 5403-94.80 is given in table 31. The day series was taken before the night series at this station. Each series contained eggs of three to four different ages. Sardine eggs can be aged without difficulty and are routinely reported by age (Ahlstrom and Kramer, 1957). Sardine spawning is confined to a limited portion of a day, usually between 8 p.m. and midnight (Ahlstrom 1943). Because of this periodicity, eggs from successive days' spawning are sharply separated in stage of development. In comparing the series taken at station 5403-94.80, eggs spawned on the night of March 23-24 are designated "A" eggs; eggs spawned on the night of March 22-23, "B" eggs; eggs spawned on the night of March 21-22, "C" eggs; and eggs spawned on the night of March 20-21, "D" eggs.

B eggs were most abundant in the day series, C eggs in the night. Since there was a fivefold increase in numbers of C eggs in the night series, which is reflected at all depths between 2 to 64 meters, there must have been a change in the water mass between the times the two series were taken. There are differences in the depth distribution of eggs of different ages. In both series the largest concentrations of B eggs were taken in the surface

TABLE 30.—Comparison of numbers of sardine and anchovy larvae taken in night and day series, grouped by size

Station	Number taken in night series in size group—				Total taken in night series	Number taken in day series in size group—				
	2.76-6.25 mm.	6.26-11.25 mm.	11.26-16.25 mm.	16.26 mm. and larger		2.76-6.25 mm.	6.26-11.25 mm.	11.26-16.25 mm.	16.26 mm. and larger	Total taken in day series
<i>Sardine (Sardinops caerulea):</i>										
4106-94.37	0	7	32	1	40	0	0	3	3	6
4106-94.47	17	44	27	1	89	14	4	4	2	24
4106-97.43	0	0	1	0	1	0	0	0	0	0
5206-90.28	4	0	1	0	5	3	0	0	0	3
5403-94.80	10	0	0	0	10	4	0	0	0	4
Total	31	51	61	2	145	21	4	7	5	37
<i>Anchovy (Engraulis mordax):</i>										
4106-94.37	0	12	12	3	27	0	3	1	0	4
4106-94.47	8	195	12	2	217	0	8	2	0	10
4106-97.43	1	4	6	1	12	0	0	0	0	0
5206-90.28	164	351	72	25	612	135	15	1	0	151
5303-91.35	0	7	5	0	12	0	0	0	0	0
5305-93.50	0	0	10	0	10	0	2	12	6	20
Total	173	569	117	31	890	135	28	16	6	185

TABLE 31.—Sardine eggs taken in replicate vertical distribution series at station 5403-94.80, by age

Day series (III: 24)					Night series (III: 24-25)						
Average depth	Number of eggs by age				Total eggs	Average depth	Number of eggs by age				Total eggs
	A	B	C	D			A	B	C	D	
2 m.....	0	58	1	0	59	2 m.....	0	35	2	0	37
7 m.....	0	49	2	0	51	7 m.....	0	17	12	0	29
18 m.....	0	21	8	0	29	17 m.....	2	17	27	0	46
28 m.....	1	13	6	0	20	27 m.....	5	12	33	0	50
41 m.....	4	9	8	0	21	42 m.....	3	9	53	0	65
53 m.....	2	5	4	0	11	52 m.....	3	7	23	0	33
68 m.....	2	2	2	1	7	64 m.....	1	2	8	0	11
102 m.....	0	1	1	1	3	101 m.....	0	0	0	0	0
135 m.....	0	0	0	0	0	127 m.....	0	0	0	0	0
201 m.....	0	0	0	0	0	200 m.....	0	0	0	0	0
Total.....	9	158	32	2	201	Total.....	14	99	158	0	271

NOTE.—A eggs—spawned on night of III: 23-24; B eggs—spawned on night of III: 22-23; C eggs—spawned on night of III: 21-22; D eggs—spawned on night of III: 20-21.

haul, and there was a fairly regular decrease in numbers with depth. C eggs had their largest concentration at 42 meters in the night series, and decreased in abundance fairly uniformly both above and below this level. The depth distribution of C eggs in day hauls corresponded fairly well to this pattern. The depth distribution of A eggs in both series was similar; the distribution of A eggs paralleled the distribution of C eggs and thus differed from that of B eggs. Hence, the differences in depth distributions of eggs of different ages were not a result of systematic changes in level with time, but must reflect differences in actual depth of spawning.

Anchovy Larvae

Nearly five times as many anchovy larvae were taken in the night series as in the day (table 6). In the night series all larvae were taken between 0 and 48 meters, corresponding to the depth distribution found for sardine larvae. In the day series, 11 larvae were obtained below 48 meters. The deeper distribution in day hauls must result from a limited vertical movement of the larvae, probably due to a negative phototropism. No larvae were taken below 88 meters in any day series. Abundance by size in day and night series is given in table 30.

The night/day ratio of anchovy larvae of different sizes is summarized below:

Size category (mm.)	Night series	Day series	N/D ratio
2.76-6.25.....	173	135	1.3
6.26-11.25.....	569	28	20.3
11.26-16.25.....	117	16	7.3
16.26 and larger.....	31	6	5.2
Total.....	890	185	4.8

There was no consistent increase in night/day ratio with size, but unlike the finding for sardine larvae, all larger sizes of larvae were considerably more abundant in night hauls than in day.

Jack Mackerel Larvae

Although jack mackerel larvae occurred in five replicate series, they were common in only one (table 7). At this station (5403-94.80) over four times as many larvae were taken in the day series as in the night. This probably resulted from a change in abundance associated with a change in water mass between the times at which the day and night series were taken. There is no close correspondence between any of the replicate series. At station 5206-90.28, 26 larvae were taken in the night series, 2 in the day series. At station 4106-94.47, seven larvae were taken in the night series, none in the day. These series suggest a high degree of contagion in the distribution of jack mackerel larvae. This species has shown no consistent difference in abundance of larvae between day and night collections taken on regular survey cruises.

Leuroglossus Larvae

Larvae of *Leuroglossus stilbius* were taken in all seven replicate series, commonly in two (table 20). At station 5206-90.28, twice as many larvae were taken in the night series, while at station 5303-91.38 where *Leuroglossus* larvae were most abundant, over six times as many larvae were taken in the night series. The night/day ratio of 5.0 for the total of all series is the highest for any species in the replicate series. The average depth

distribution of *Lewroglossus* larvae in day and night series was as follows:

Average depth	Day series		Night series	
	Number	Percent	Number	Percent
2 m.....	0	0	3	0.5
8 m.....	0	0	0	0
19 m.....	0	0	1	.2
28 m.....	0	0	25	4.4
41 m.....	7	6.2	15	2.6
56 m.....	8	7.1	128	22.5
72 m.....	29	25.7	272	47.7
105 m.....	40	35.4	28	4.9
138 m.....	24	21.2	13	2.3
215 m.....	3	2.7	63	11.1
285 m.....	2	1.8	22	3.9
Total.....	113	100.1	570	100.1

In night hauls, the larvae occurred at somewhat shallower depths: 29 larvae were taken above 34 meters at night, none in day hauls. The center of abundance was between 48 and 88 meters in night hauls, while in day hauls it was between 64 and 175 meters. However, more larvae were taken below 88 meters in night hauls than in day: 126 in night hauls, 69 in day hauls. Some migration to deeper levels is indicated for day hauls, but the migration appears to be of moderate extent and within the zones being sampled in taking the vertical distribution series.

Hake Larvae

Hake larvae were common in only one replicate series (5403-94.80), although they occurred in five (table 9). At three stations, larvae were taken only in the night series (one to eight larvae). In the series at station 5403-94.80, most of the larvae taken in the night series occurred at one level (68 meters); in all other hauls taken between the surface and approximately 105 meters, there were more larvae in the day series than in the night at this station (fig. 10, a and b). The night/day ratio of 2.5 for hake larvae is so markedly influenced by one haul that little reliance can be placed on this ratio. Hake larvae had similar depth ranges in both the day and night series.

Sebastes Larvae

There is no clear-cut evidence that *Sebastes* larvae are taken in greater numbers in night hauls than in day hauls. Of the five replicate series in which rockfish larvae were common (table 10), the largest numbers were taken in day series at three stations. In fact, were it not for the large difference found at station 5303-91.38 (225 larvae

in night series, 46 in day) the night/day ratio would be less than 1. In most series there is no consistent difference in depth distribution between the day and night series. At station 5303-91.38 the larvae occurred somewhat deeper in the night series than in the day, while at station 5305-93.50 most rockfish larvae occurred at notably shallower depths in the night series than in the day.

Lanternfish Larvae

Larvae of *Lampanyctus leucopsarus* occurred in all seven replicate series, commonly in three (table 14). At station 93.50 the larvae had identical depth ranges in the day and night series, but larger numbers of larvae were taken in the day hauls. At stations 5206-90.28 and 5303-91.38, larger numbers were taken in the night series. Because of the unusual concentration of larvae at one level in series 5206-90.28 (94 percent of total taken in haul averaging 27 meters deep), this series has been strongly influenced by localized clumping of larvae. The clumping may have resulted from a vertical concentration of larvae that was missed in daytime sampling, or a horizontal concentration that was missed in daytime due to a change in the water mass. The night/day ratio of 1.8 was strongly influenced by this haul; without the day and night hauls from this level at station 5206-90.28 the night/day ratio for replicate series would approximate 1.

Larvae of *Lampanyctus mexicanus* occurred in six replicate series, usually in small numbers (table 15). In each instance, more larvae were taken in night series than in day, and the larvae had a somewhat shallower depth distribution in night series. Larvae of *L. mexicanus* in the replicate series were limited to four levels with average depths of 19, 28, 41, and 56 meters. Approximately 83 percent of the larvae taken in night series occurred at the 19- and 28-meter levels, while 70 percent of the larvae taken in day series occurred at the 41- and 56-meter levels.

Larvae of *Lampanyctus ritteri* occurred in small numbers in all seven replicate series (table 16). The night/day ratio is only slightly greater than 1. It is difficult to reconcile this finding with the night/day ratio of 14.4 based on repeated hauls taken at station 5010-70.130. There is no consistent difference in depth of occurrence between day and night series.

Discussion

In summary, there are marked differences in abundance of sardine, anchovy, and *Leuroglossus* larvae in night collections as compared with day collections. For all three species, there is evidence of a limited vertical migration, but no evidence that the larvae migrate below the levels sampled.

Most other species (*Sebastes*, lanternfish, hake) were taken in somewhat larger numbers, on the average, in night collections, but not necessarily so at any given station. The larvae of most of these were taken at approximately the same levels in day and night series, but larvae of *Lampanyctus mexicanus* occurred somewhat deeper in day hauls than in night. Abundance of jack mackerel larvae does not appear to be affected by time of collection.

There are a number of papers which have called attention to the disparity between day and night catches of larvae, particularly clupeid larvae. Bridger (1956), for example, reported that seven times as many herring larvae were taken in night collections as in day collections during five cruises made in 1952 and 1953. Bridger has summarized much of the previous work on day and night variation in catches of fish larvae. F. S. Russell (1926, 1928, and others) has done the most extensive research in this field. A rather typical finding reported by Russell (1926) was the difference in pilchard catches between night and day series taken on July 15-16, 1924: pilchard larvae 5 to 10 mm. in length were 6.0 times as abundant in night collections, larvae between 11 and 20 mm. in length were 13.9 times as abundant.

Both Silliman (1943) and Ahlstrom (1954) have suggested that the lower catches of larvae during daylight hours must result from avoidance of the net by the larger larvae. Bridger (1956: 55) came to the same conclusion. He stated that "On the evidence presented it seems almost certain that the lower catches by day are due to the ability of the larger larvae to avoid the nets in daytime. This would explain the increasing night/day ratio obtained as the larvae develop and become more agile."

SUMMARY

Information is given on the vertical distribution of 46 kinds of fish larvae and 8 kinds of fish eggs, based on 22 vertical distribution series made

off southern California and central Baja California in 1941 and 1952 through 1955. Each series consisted of 6 to 11 hauls taken with closing gear at successively deeper levels.

Most fish larvae were found to occur in the upper mixed layer and in the upper part of the thermocline between the surface and approximately 125 meters. Of the 15 most common kinds of larvae taken in vertical distribution series, 12 occurred within this depth range.

All of the more common kinds of larvae showed marked differences in their vertical distribution from series to series.

Larvae of the four pelagic fishes of considerable commercial importance in California—Pacific mackerel, Pacific sardine, jack mackerel, and northern anchovy—had the shallowest depth distributions of any of the more common kinds sampled. Between 79 and 99 percent of the larvae of these species occurred above 50 meters.

Rockfish larvae were as commonly taken within the thermocline as above, but they were not taken below the thermocline. Larvae of *Citharichthys* spp. were taken between the surface and 88 meters.

Larvae of lanternfish (myctophids) were seldom taken in the upper 23 meters. Larvae of the three most common species of *Lampanyctus* in the CCOFI survey area (*L. leucopsarus*, *L. mexicanus*, and *L. ritteri*) occurred mostly between 24 and 64 meters. Larvae of *Electrona* spp. were found to have the deepest distribution of the lanternfish studied. The gonostomatid, *Vinciguerria lucetia*, occurred between the surface and 122 meters, with the largest concentrations occurring between 24 and 48 meters.

Three common kinds of larvae occurred in greatest abundance within or below the thermocline: *Merluccius productus* (hake), *Leuroglossus stilbicus*, and *Bathylagus wesethi*. The depth distribution of *Leuroglossus* larvae was not completely covered by hauls extending to approximately 285 meters.

Temperature data are given for the more common fish larvae taken in vertical distribution series.

Replicate vertical distribution series were taken at seven stations, one in daylight hours, the other during darkness. More larvae were taken in the night series at six stations; the night/day ratio for the seven series combined was 2.3. Larvae of *Leuroglossus*, anchovy, and sardine showed the

most marked differences between day and night series (4 to 5 times as many as in night series, on the average). Most other species (*Sebastes*, lanternfish, hake) were taken in somewhat larger numbers, on the average, in night collections, but not necessarily so at any given station. Abundance of jack mackerel larvae did not appear to be affected by time of collection.

Diurnal differences in abundance of larvae have been observed also in regular survey collections, and in studies involving repeated occupancies of a station. An example of the latter is discussed—repeated occupancies of station 70.130 at 3-hour intervals for an 8-day period in October 1950. The night/day ratio for all larvae collected in 63 hauls at this station was 3.6; the variation in night/day ratios for individual species was from 1.7 to 14.4.

A comparison of the catches at two levels on Norpac (upper, 0–131 meters; lower, 131–262 meters) supplemented data obtained from vertical distribution series; 26 kinds of larvae occurred in both Norpac material and vertical series. About one-ninth as many larvae were taken in the 131 to 262-meter level as in the 0 to 131-level on Norpac. Half of the larvae taken in the deeper level belonged to a single genus, *Argyropelecus*; in addition, seven other kinds of larvae had 20 percent or more of their numbers in this level on Norpac.

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APPENDIX

Haul data for the 22 series of closing net hauls are given in the following table. It is included in an appendix rather than in the text because of its length. For each series the following information is given.

Station position is the position at the beginning of a series. At intervals during a series the vessel was brought back to the starting position, but some hauls were taken several miles away from the position listed.

Station number, as for example, 4105–92.39. The first group of figures identifies the year and month of collection. Thus, 4105 refers to collec-

tions made in 1941 during the fifth month. The second group identifies geographic position in an arbitrary but consistent numbering system of a grid pattern, oriented roughly parallel to the general trend of the coastline along California and Baja California. The figures before the decimal in the second group refer to the station line, those following to position on the line. The pivotal station in the grid is station 80.60 (34°09' N., 121°09' W.) located about 40 miles offshore from Point Conception. The coastwise base line through this point has a true bearing of 330°. Station lines are oriented at right angles to the base line on a mercator projection. Numerical value assigned to a station line increases to the south of the pivotal station (or decreases to the north) at the rate of 12 miles for each unit. The numerical value assigned to a station on the line increases (or decreases) by one unit for each 4-mile interval from the base line (drawn through station 80.60).

Date, midtime of haul, and duration of haul in minutes are self-explanatory.

Wire out. When two values are given for wire out, such as 140-160 meters, the net was opened with the longer length of cable payed out (160 meters, in the example), raised in steps during the haul to the lesser value (140 meters) and closed at this depth before being brought to the surface.

Range in depth is the shallowest and deepest depth reached by the net during a haul, determined from the cosine of the angle of stray of the towing wire from the vertical, multiplied by the length of the towing cable. Determinations of the angle of stray of the towing wire were made at minute intervals in 1941, at half-minute intervals in 1952 through 1955.

Middepth of haul is the average of the depth determinations (usually 15 to 20) made for each haul.

Temperature determinations are based on bathythermograms. Usually three bathythermograph casts were made for each series—one immediately before, one during, and one immediately after completing a series.

APPENDIX TABLE 1.—Data on 22 series of closing net hauls for determining the vertical distribution of fish eggs and larvae

Station and haul	Date	Midtime of haul	Duration of haul (min.)	Wire out (m.)	Middepth of haul (m.)	Range in depth (m.)	Temperature at middepth (° C.)
Position, 32°29' N., 119°26' W.:							
4104-91.54-1	IV-30-41	1718	16	4	3	0-3	15.0
2	do.	1746	16	10-15	8	6-12	15.0
3	do.	1816	16.5	25-30	18	15-25	14.8
4	do.	1846	16.5	35-40	24	14-29	14.8
5	do.	1943	16.5	55-60	37	28-42	14.6
6	do.	2011	15.5	75-85	54	44-62	13.0
7	do.	2040	15.5	100-110	72	65-92	11.4
Position, 33°20' N., 118°33' W.:							
4105-89.38-1	V-2-41	0815	15	4	3	0-3	17.2
2	do.	0845	16	10-15	8	5-14	17.1
3	do.	0909	16	25-30	18	15-21	16.6
4	do.	1001	16	35-40	25	19-31	16.1
5	do.	1026	16	55-60	36	30-43	15.0
6	do.	1318	16	75-85	56	48-70	12.8
7	do.	1348	15.5	100-110	73	65-87	11.5
Position, 32°50' N., 118°18' W.:							
4105-92.39-1	do.	2005	15	4	3	0-4	17.1
2	do.	2038	16	10-15	10	7-13	16.3
3	do.	2106	16	25-30	20	17-26	16.1
4	do.	2132	16	35-40	28	25-33	15.4
5	do.	2200	17	55-60	40	30-53	13.5
6	do.	2230	15	75-85	58	52-73	11.4
7	do.	2300	15.5	100-110	76	68-98	10.7
8	do.	2348	15.5	140-160	112	97-142	9.8
Position, 32°23' N., 117°52' W.:							
4106-94.37N-1	VI-17-41	2215	16.5	4	3	0-3	16.8
2	do.	2318	17	10-15	9	7-12	16.5
3	do.	2353	17.5	25-30	20	15-24	16.0
4	VI-13-41	0037	17	35-40	27	22-35	15.4
5	do.	0111	17	55-60	41	36-52	14.1
6	do.	0144	16	75-85	58	48-84	11.9
7	do.	0222	17.5	100-110	69	57-101	10.9
8	do.	0312	17.5	140-160	100	90-146	9.8
Position, 32°17' N., 117°52' W.:							
4106-94.37D-1	do.	0906	16	4	3	0-3	17.2
2	do.	0944	17	10-15	9	6-12	17.0
3	do.	1014	17	25-30	19	14-21	16.3
4	do.	1044	17.5	35-40	30	25-36	15.2
5	do.	1114	18	55-60	41	38-43	13.8
6	do.	1147	18	75-85	58	52-67	12.2
7	do.	1223	17.5	100-110	73	68-81	11.2
8	do.	1310	17	140-160	105	99-152	9.7
9	do.	1352	17	190-210	139	125-156	9.2

APPENDIX TABLE 1.—Data on 22 series of closing net hauls for determining the vertical distribution of fish eggs and larvae—Con.

Station and haul	Date	Midtime of haul	Duration of haul (min.)	Wire out (m.)	Middepth of haul (m.)	Range in depth (m.)	Temperature at middepth (° C.)
Position, 32°12' N., 118°38' W.:							
4106-04.47N-1	do.	2116	15	4	3	0-4	15.8
2	do.	2145	17	10-15	10	7-13	15.8
3	do.	2216	17	25-30	21	18-25	15.2
4	do.	2248	17.5	35-40	27	24-32	14.5
5	do.	2321	18	55-60	44	38-52	12.8
6	do.	2352	16	75-85	59	52-69	11.1
7	VI-19-41	0028	16.5	100-110	76	66-108	9.9
8	do.	0107	17	140-160	107	90-149	9.1
9	do.	0148	17	190-210	141	122-208	8.7
Position, 32°10' N., 118°39' W.:							
4106-04.47D-1	do.	0834	15	4	3	0-3	15.7
2	do.	0858	16.5	10-15	9	7-14	15.6
3	do.	0925	18	25-30	21	17-25	14.9
4	do.	0952	17	35-40	28	23-36	14.5
5	do.	1018	17	55-60	42	36-47	13.3
6	do.	1045	16	75-85	60	52-69	10.9
7	do.	1118	17	100-110	76	70-85	10.2
8	do.	1153	18	140-160	110	99-121	9.0
9	do.	1236	17.5	190-210	141	120-188	<8.8
Position, 31°55' N., 118°03' W.:							
4106-07.43N-1	do.	2145	15	4	3	0-3	(*)
2	do.	2209	17	10-15	10	7-14	(*)
3	do.	2235	17	25-30	21	17-25	(*)
4	do.	2305	17	35-40	27	24-32	(*)
5	do.	2332	17	55-60	43	39-50	(*)
6	VI-20-41	0002	16	75-85	57	50-62	(*)
7	do.	0036	16.5	100-110	79	67-100	(*)
8	do.	0105	16.5	140-160	106	90-133	(*)
9	do.	0202	17	190-210	142	127-168	(*)
Position, 31°55' N., 118°03' W.:							
4106-07.43D-1	do.	0828	15	4	3	0-3	(*)
2	do.	0854	17	10-15	10	7-13	(*)
3	do.	0920	17	25-30	20	18-22	(*)
4	do.	0946	17	35-40	28	24-32	(*)
5	do.	1040	17	55-60	42	36-47	(*)
6	do.	1138	17	75-85	60	57-64	(*)
7	do.	1209	16	100-110	77	70-85	(*)
8	do.	1344	16.5	140-160	104	92-119	(*)
9	do.	1406	17	190-210	133	120-172	(*)
Position, 33°28.5' N., 117°46.7' W.:							
5206-00.28N-1	VI-12-52	2224	10	3	2	0-3	16.6
2	do.	2157	10	10	7	7-8	16.6
3	do.	2258	10	25	17	15-19	14.7
4	VI-13-52	0005	10	40	27	21-35	12.1
5	do.	0034	10	60	42	39-44	10.1
6	do.	0108	10	80	57	54-59	9.7
7	do.	0140	10	100	73	68-80	9.2
8	do.	0210	10	150	107	104-111	9.2
9	do.	0248	10	200	142	136-146	8.9(131 m.)
10	do.	0330	10	300	206	189-216	(*)
11	do.	0415	10	400	286	268-302	(*)
Position, 33°28.5' N., 117°46.7' W.:							
5206-00.28D-1	do.	0918	10	3	2	0-3	18.2
2	do.	0940	10	10	7	5-8	16.4
3	do.	1000	10	25	18	16-19	15.1
4	do.	1025	10	40	29	26-32	11.2
5	do.	1112	10	60	44	41-47	10.0
6	do.	1135	10	80	56	54-58	9.9
7	do.	1200	10	100	71	64-76	9.7
8	do.	1228	10	150	105	100-111	9.4
9	do.	1305	10	200	134	112-141	9.4
10	do.	1425	10	300	216	208-223	(*)
11	do.	1500	10	400	286	278-292	(*)
Position, 28°05.5' N., 114°57.5' W.:							
5208-120.35-1	VIII-17-52	0302	5	5	3	2-4	19.7
2	do.	0323	5	15	10	10-11	19.6
3	do.	0339	5	25	18	14-22	18.9
4	do.	0401	5	40	27	22-30	18.4
5	do.	0426	5	55	36	30-40	17.8
6	do.	0452	5	70	51	49-53	16.1
Position, 33°02' N., 118°23' W.:							
5303-01.38N-1	III-4-53	2005	10	3	2	0-3	14.4
2	do.	2031	10	10	7	6-9	14.4
3	do.	2115	10	25	18	16-20	14.3
4	do.	2137	10	40	29	25-33	14.3
5	do.	2247	10	60	41	37-46	14.2
6	do.	2316	10	80	54	51-58	14.0
7	do.	0022	10	100	68	60-77	11.6
8	III-5-53	0100	10	150	106	96-118	9.8
9	do.	0128	10	200	150	131-168	9.4
10	do.	0218	10	300	211	197-230	9.0
11	do.	0329	10	400	291	262-311	
Position, 33°02' N., 118°23' W.:							
5303-01.38D-1	do.	0620	10	3	2	0-3	14.2
2	do.	0642	10	10	7	6-8	14.2
3	do.	0702	10	25	18	15-20	14.1
4	do.	0724	10	40	28	24-32	14.0
5	do.	0753	10	60	42	27-47	13.9
6	do.	0817	10	80	56	51-61	13.2
7	do.	0843	10	100	72	64-83	10.7
8	do.	0910	10	150	92	82-102	9.9
9	do.	0945	10	200	139	131-141	9.3
10	do.	1018	10	300	206	197-212	8.6

*No temperature data available.

APPENDIX TABLE 1.—Data on 22 series of closing net hauls for determining the vertical distribution of fish eggs and larvae—Con.

Station and haul	Date	Midtime of haul	Duration of haul (min.)	Wire out (m.)	Middepth of haul (m.)	Range in depth (m.)	Temperature at middepth (° C.)	
Position, 32°10.5' N., 118°57' W.: 5305-93.50N-1	V-25-53	2045	10	3	2	0-3	13.9	
	2	2182	5	10	6	6-7	14.2	
	3	2145	5	25	21	20-22	13.4	
	4	2157	5	40	29	27-33	13.4	
	5	2212	5	60	43	29-48	12.5	
	6	2225	10	80	57	55-62	11.2	
	7	2247	10	100	70	62-78	10.6	
	8	2310	10	150	106	96-110	9.3	
	9	2357	10	200	138	123-146	9.0	
	10	V-26-53	0033	10	300	222	189-243	8.4
	11	0109	10	400	276	252-302	7.8	
Position, 32°10.5' N., 118°57' W.: 5305-93.50D-1	do	0715	5	3	2	0-3	14.9	
	2	0722	5	10	7	6-7	14.4	
	3	0735	5	25	16	14-16	14.1	
	4	0748	5	40	25	24-27	13.5	
	5	0759	5	60	33	25-33	13.2	
	6	0845	5	80	46	40-54	12.5	
	7	0924	10	100	63	42-73	11.0	
	8	0945	10	150	103	82-120	9.9	
	9	1029	10	200	138	131-143	9.4	
	10	1159	10	300	239	230-252	(*)	
	Position, 30°58.5' N., 120°45' W.: 5403-94.80N-1	III-24-54	2030	10	3	2	0-3	14.3
2		2102	10	10	7	6-7	14.3	
3		2125	10	25	17	16-18	14.3	
4		2143	10	40	27	24-29	14.3	
5		2308	10	60	42	39-48	14.3	
6		2331	10	80	52	44-57	14.3	
7		III-25-54	0000	10	100	64	53-72	14.1
8		0025	10	150	101	96-106	10.8	
9		0135	10	200	127	118-141	9.9	
10		0215	10	300	200	176-208	8.7	
Position, 30°58.5' N., 120°45' W.: 5403-94.80D-1		III-24-54	0908	10	3	2	0-3	14.1
	2	0940	10.5	10	7	6-7	14.1	
	3	1005	10	25	18	17-19	14.1	
	4	1025	10.5	40	28	26-29	14.0	
	5	1105	10	60	41	39-42	14.0	
	6	1140	10.5	80	53	50-60	14.0	
	7	1232	10.5	100	68	59-72	13.2	
	8	1305	10.5	150	102	96-110	11.1	
	9	1350	10	200	135	126-141	9.7	
	10	1425	10.5	300	201	193-219	8.6	
	Position, 28°51.5' N., 119°22.5' W.: 5504-107.80-1	IV-16-55	1355	10	3	2	0-3	15.7
2		1430	10	10	8	6-10	15.7	
3		1455	10	25	20	18-22	15.7	
4		1515	10	40	31	27-26	15.7	
5		1535	10.5	60	45	40-50	15.7	
6		1600	10	80	57	54-63	15.3	
7		1620	10	100	70	63-81	15.0	
7A		1640	10.5	125	83	79-88	14.3	
8		1720	10	150	111	104-124	13.8	
9		1745	10.5	200	142	129-149	12.5	
Position, 28°56.5' N., 117°39' W.: 5504-110.60-1		IV-23-55	1155	10	3	2	0-3	15.6
	2	1220	10	10	7	6-8	15.6	
	3	1235	10	25	18	19-20	15.6	
	4	1255	10	40	29	26-32	15.6	
	5	1315	10	60	44	39-50	15.6	
	6	1330	10	80	58	54-63	15.6	
	7	1400	10.5	100	73	64-86	15.4	
	7A	1420	9.5	125	83	77-100	15.3	
	8	1440	9.5	150	105	100-110	13.2	
	Position, 27°33' N., 115°52.5' W.: 5504-120.50-1	IV-18-55	2015	10	3	2	0-3	15.3
		2	2045	10	10	7	6-8	15.3
3		2100	10	25	18	16-22	15.3	
4		2120	10	40	27	25-33	15.3	
5		2135	10	60	44	39-49	15.3	
6		2155	10	80	60	52-66	14.1	
7		2215	10	100	74	66-86	12.2	
7A		2235	10	125	99	85-107	10.8	
8		2300	10	150	110	100-123	10.8	
9		2355	11.5	200	137	123-164	10.8	
10		0025	11	300	225	208-270	-----	
Position, 25°29' N., 115°24' W.: 5504-130.60-1	IV-21-55	2325	10	3	2	0-3	16.6	
	2	0005	10	10	8	7-8	16.55	
	3	0020	10.5	25	17	14-21	-----	
	4	0035	10	40	28	24-32	-----	
	5	0050	10	60	42	36-46	-----	
	6	0110	10	80	56	54-61	-----	
	7	0125	10	100	72	66-76	-----	
	7A	0145	10.5	125	89	84-100	-----	
	8	0205	10.5	150	102	98-106	-----	
	9	0230	10.5	200	136	129-141	-----	
	10	0330	10.5	300	215	205-230	-----	

*No temperature data available.

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VARIABILITY OF SKIPJACK RESPONSE TO LIVE BAIT

By HEENY S. H. YUEN



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ABSTRACT

Observations made from commercial skipjack live-bait fishing boats, operating from Honolulu, revealed that catch rates for each school of skipjack had a general pattern: the rates rose to a peak and then declined with elapsed fishing time. In this paper, peak catch rate and duration of fishing after the peak were selected as measures of biting response and were compared with data on location, the weather, time of day, and stomach contents. With a fork length of 60 cm. as the dividing line between small and large skipjack, the peak catch rates for small fish were higher than those for large fish, but this was attributed to the greater ease of catching small fish. The peak catch rate of large skipjack increased with the distance from land. The postpeak duration of fishing for large skipjack was found to be negatively correlated with volume of stomach contents and relative time since the last major feeding. Large skipjack feeding on fast-swimming fish seemed to show a better response to chum (live bait) than did those feeding on slow-swimming fish. Weather conditions did not seem to affect the peak catch rate or the postpeak duration. The relation of biting response to time of day was not obvious.

VARIABILITY OF SKIPJACK RESPONSE TO LIVE BAIT

By Heeny S. H. Yuen, *Fishery Research Biologist*, BUREAU OF COMMERCIAL FISHERIES

Fishermen in the Hawaiian Islands chum live bait to attract skipjack (*Katsuwonus pelamis*) to the ship and to hold them there. The reaction of skipjack to chumming may vary from no response to feverish feeding activity which results in a sizable catch. In reporting the results of live-bait fishing aboard research ships of the Pacific Oceanic Fishery Investigations¹ in Hawaiian waters, Royce and Otsu (1955) stated that fish were caught from only 43 percent of the schools chummed. Time and bait expended on nonresponding schools represent a considerable economic loss to the fishermen, particularly because of the short supply of bait.

If the efficiency of the fisherman is to be improved, the factors which contribute to the variability of skipjack responses to chum should be ascertained. A prerequisite to this would be to measure the extent of variability of biting behavior. It is the intent of this study to measure and determine the reasons for the variability of skipjack response to chum.

Perhaps the measure of variability of response will have further application. For instance, it may be used to evaluate the success of new bait species and artificial baits, or to compare the response of skipjack in unexploited areas to that of present commercially successful areas.

Factors influencing the biting behavior of skipjack, as presented by past studies, may be classified as environmental, physiological, and psychological or perhaps psychophysiological. Among the environmental factors in the Japanese skipjack fishery, Imamura (1949) mentioned water clarity, current velocity, weather, abundance of natural food, and time of day. Transparency, chlorinity, and temperature of the water are advanced by Uda (1940b) as affecting skipjack catches, but probably as migrational rather than response determinants. Uda (1940a) and Suyehi

hiro (1938) also mentioned time of day as a factor. The latter also noted the effect of seasons and the proximity of land on biting behavior.

The first physiological factor that comes to mind when considering biting response is the state of hunger. Both Uda (1933) and Suyehiro (1938) investigated its effect; the former in terms of fullness of the stomach and the latter in terms of time since last feeding. That the state of gonad development may also be a factor is indicated by Brock (1954) who reported a dearth of ripe individuals despite extensive sampling of the Hawaiian skipjack fishery.

The factor that was considered as a psychological or psychophysiological one was the possible preference of the skipjack for certain species of prey or perhaps for prey with certain types of behavior. This possibility was conjectured because of Suyehiro's (1938) statement that skipjack feeding on pelagic forms responded to chum better than those feeding on inshore forms. The effect of school size, if any, would also fall in this category.

The size of the skipjack and the fishing effort measured by the number of hooks fished were also considered as possible factors.

Since the data were collected by investigators who were permitted aboard commercial vessels with the provision that they would not interfere with the fishing operations, not all of the possible factors mentioned could be measured. Unfortunately, the data not collected fell in the environmental category.

Operations on a skipjack sampan are not geared to accommodate observers, but the following captains and crews went out of their way to make us comfortable and to help us collect our materials: Yoshiichi Teramae and crew of the M/V *Neptune*, Tsuruichi Sarae and crew of the M/V *Orion* (1956), Richard Kinney and crew of the M/V *Orion* (1957), Noboru Tsue and crew of the M/V *Buccaneer*, Tom Fukunaga and crew of the M/V *Angel*, and Kuniyoshi Asari and crew of the M/V *Marlin*.

NOTE.—Approved for publication September 26, 1958.

¹ Redesignated Bureau of Fisheries Biological Laboratory, Honolulu, effective January 1, 1959.

METHODS

COLLECTION OF DATA

Data were collected by observers who accompanied skipjack sampans throughout the 1956 and 1957 skipjack seasons, April through September, at about weekly intervals. Only the more successful and larger of the sampans were chosen because the probabilities of getting data would be enhanced and the larger deck permitted collection of materials with less interference to fishing operations.

A review of fishing operations described in greater detail by June (1951) follows: the boat leaves port early enough to be at a promising fishing area at daybreak. It is usually held on an arbitrary course while the scouts scan the ocean for birds that flock over fish schools. When a flock is sighted, the boat is steered to head it off. On reaching the head of the flock, the boat is slowed, water sprays are turned on, and chumming is started. The bait is dribbled out as evenly as possible until signs of surfacing fish are seen astern. When the fish begin to surface, the chummer intensifies the chumming until the fish are directly at the stern within reach of the hooks, at which time he reduces the rate of chumming to what he considers a minimum to keep the school at the boat. If the school moves away without responding, chumming is stopped and the boat accelerated to get into position for another attempt. As soon as the school has been successfully lured to the boat, the fishermen get into position at the stern and start fishing. The school is fished until the bait supply is exhausted or until the captain decides that the rate of catching is too slow to be worth while. The catch is stored as soon as fishing is stopped, and the boat then proceeds homeward or to look for more schools depending on the bait supply and hour of day.

The fishing of 92 skipjack schools was observed. Recording of data started with the sighting of a flock. The time of sighting was recorded to the nearest minute. During the approach a description of the weather was recorded. It included the height of the waves, an estimate of wind velocity and direction, the type of clouds and amount of sky covered, and light conditions. "Light" was described as bright sun, cloudy-bright, hazy, dull, and raining.

A running description of the activity of the flock was kept during the approach, and when the boat was close enough an estimate was made of the number in each flock and the species. The flocks were described as flying high, diving, scattering, regrouping, enlarging, etc. In the beginning, attempts were made to estimate the direction and velocity of the flocks but these were abandoned as being unreliable. As soon as contact with the school was made, its location was approximated.

The times of the following events were recorded to the nearest 5 seconds: (1) the beginning and end of each pass, (2) the first signs of fish surfacing in response to the chum, (3) the start of fishing, and (4) the landing of the first fish. During the few instances when the slowing of the boat and the start of chumming did not coincide, the latter was considered to be the start of the pass. The placement of hooks in the water signified the start of fishing.

As fish were caught, each was tallied on a counter. At the end of each minute (when the second hand pointed to 12) the reading was recorded with the time. If fishing did not start exactly on a minute, an error with a limit of plus or minus 30 seconds was introduced in the first minute. On earlier trips the catch was recorded at 2-minute intervals. Occasionally an individual fisherman left his post to change his fishing pole or to perform other duties such as helping the chummer, or to gaff fish. Each change in the number of men fishing and the time was noted, except when a man went to change his pole, a temporary absence.

The possibilities for error, especially when the fish were landed rapidly, were ever present with the observer watching the time, tallying the number of fish caught, accounting for the movements of the fishermen, and recording. Another method which decreased the amount of work during the hectic time of fishing and thereby reduced the possibilities of error was later used. This included the use of a movie camera with a single-frame trigger and a marine clock with white numerals against a black background. These were mounted facing each other (fig. 1). The shutter was released as each fish was caught, resulting in an exact record of the time of capture. The number of frames used corresponded to the number of fish

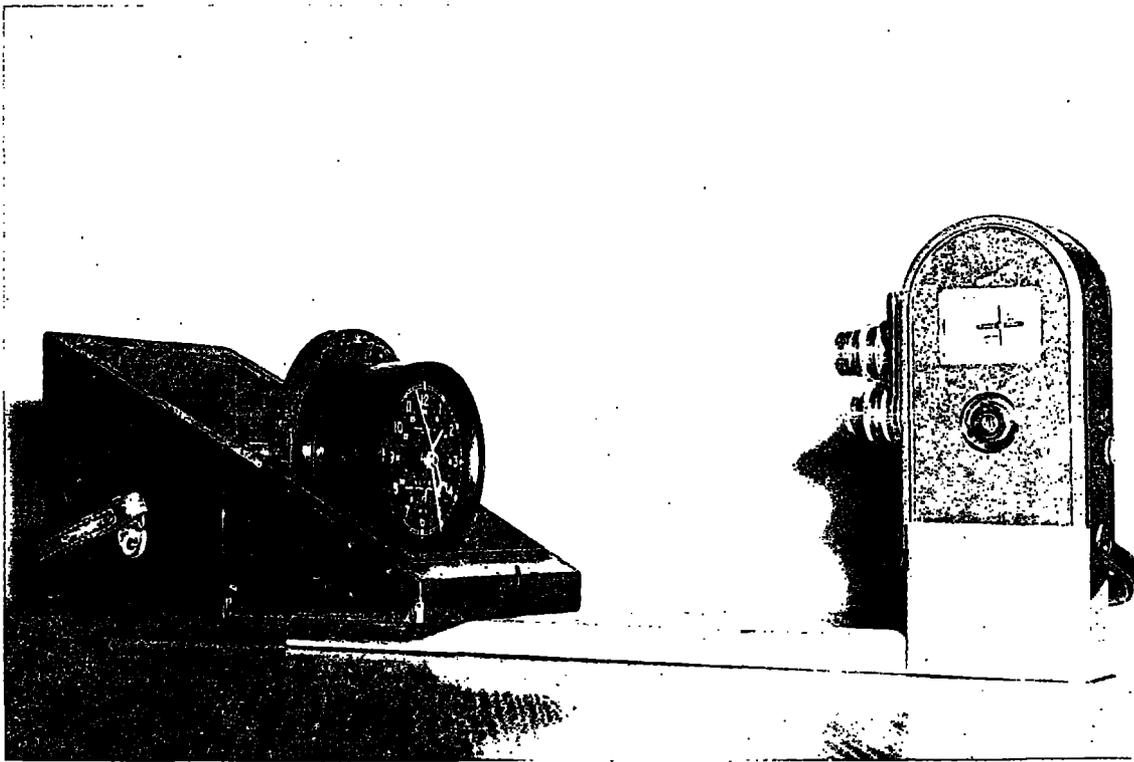


FIGURE 1.—Photograph of clock and camera setup.

caught. An additional hand on the clock was manipulated to point to the numeral corresponding to the number of men fishing at any time.

The precision of this system depended on the speed at which the single-frame trigger could be operated. The smallest possible interval of time between frames was 0.6 second. This means that when several fish were caught simultaneously, the record would indicate that they were caught 0.6 second apart.

At the cessation of fishing, the skipjack were randomly sampled. At first the sample size was 20, but this was later reduced to 10. The sample comprised the entire catch when the catch was less than the prescribed sample size.

The fork length of each fish in the sample was taken, then the stomach and a piece of the gonads were removed and placed in a muslin bag. The stomach was punctured while in the bag and the bag secured and placed in approximately 10-percent formalin. Five hundred and thirteen fish, representing 43 schools, were treated in this manner.

During the period between the 1956 and 1957 seasons, the personnel of the M/V *Buccaneer* collected 60 stomach samples from 6 schools. The data collected with the samples included: (1) the location of the school, (2) the time of fishing, (3) an estimate of the weight of the total catch from the school, (4) an estimate of the average weight of the fish, and (5) a statement of whether fish response was good, fair, or poor.

TREATMENT OF DATA

The rate at which the fish were caught, in terms of fish per hook-minute, was calculated for each minute of elapsed fishing time for the schools observed later in the study. For the schools observed earlier, the nature of the data did not permit the rates to be calculated for intervals of less than 2 minutes.

In the identification of the stomach contents the fish were placed in their families, mollusks in their suborders, and crustaceans in their orders. The individuals in each category were counted. The volume for each category was ascertained by water

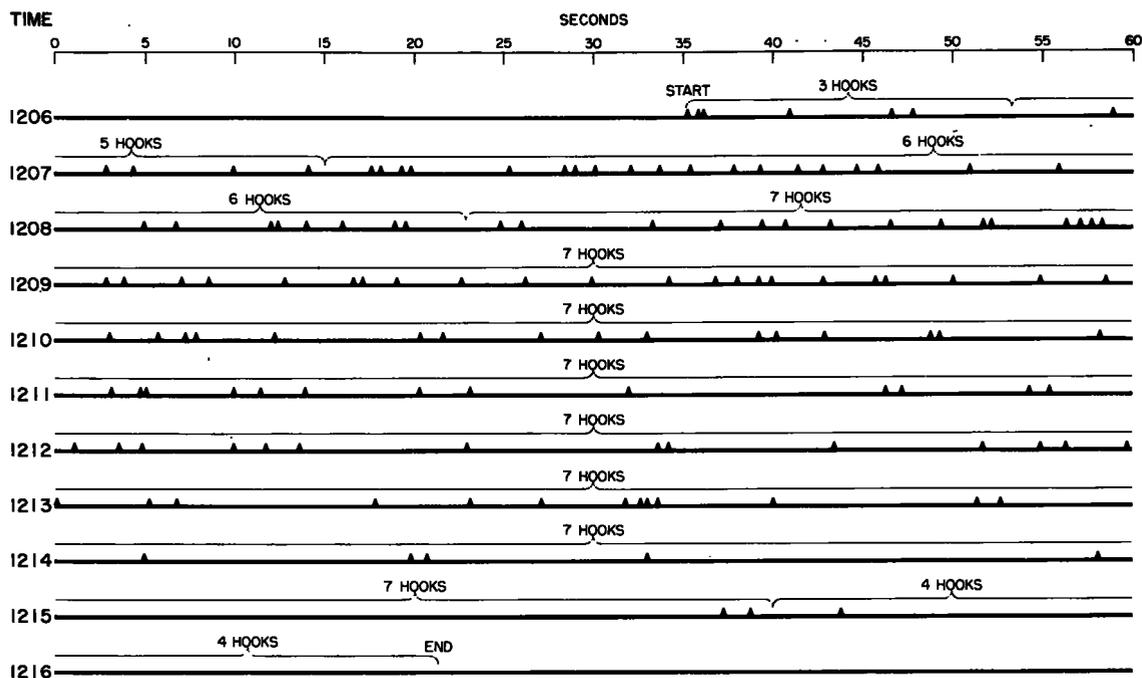


FIGURE 2.—Plot of the landing of individual skipjack, and time. Each mark represents one skipjack.

displacement to the nearest 0.1 ml. or with an error of about 1 percent depending on the volume. In addition, all fish were ranked by relative stage of digestion.

The fork lengths of the smallest and largest fish in each family from each sample of stomachs were measured. This disclosed the size range of each fish family consumed by an individual skipjack school. The lengths of the squid mantles were likewise measured. Linear measurements of other items were not attempted.

Digested remains were identified whenever possible as fish, mollusks, or crustacean. Otherwise they were classified as "gurry." Volumetric measurements were taken as described earlier.

The bait found in stomachs received the same treatment as other fish, but the results were discarded as unreliable because skipjack often regurgitate much of the bait as they are caught or soon after. At times food deeper in the stomach is also regurgitated but the amount seems negligible.

Trematodes, nematodes, and Acanthocephala were found in the stomachs in small quantities. These were assumed to be parasites and were not considered.

RESULTS

GENERAL INFORMATION ON FISHING

No fish were caught from 52 percent of the schools chummed.

The rate at which the skipjack took the hooks varied. More often than not the fish seemed to bite in short flurries (fig. 2). This may be due to the distributional makeup of skipjack schools. In the few times when the fish could be clearly seen in the water, the schools seemed to be aggregates of many small groups of about 10 fish each.

When the catch rates are plotted against elapsed fishing time at 1- or 2-minute intervals (fig. 3), they present an assortment of shapes. In general there is a rise to a peak with a subsequent decline. Figure 3, *A* shows a relatively early peak, with irregular rise and decline and is typical of most of the plots. Occasionally there are variations as seen in figure 3: *B* illustrates a later peak; *C* has a sharper decline; and *D*, the major peak, is not particularly dominant. *E* is an example of a school that responded poorly. An average of 32.7 percent of the total catch was made during the prepeak period.

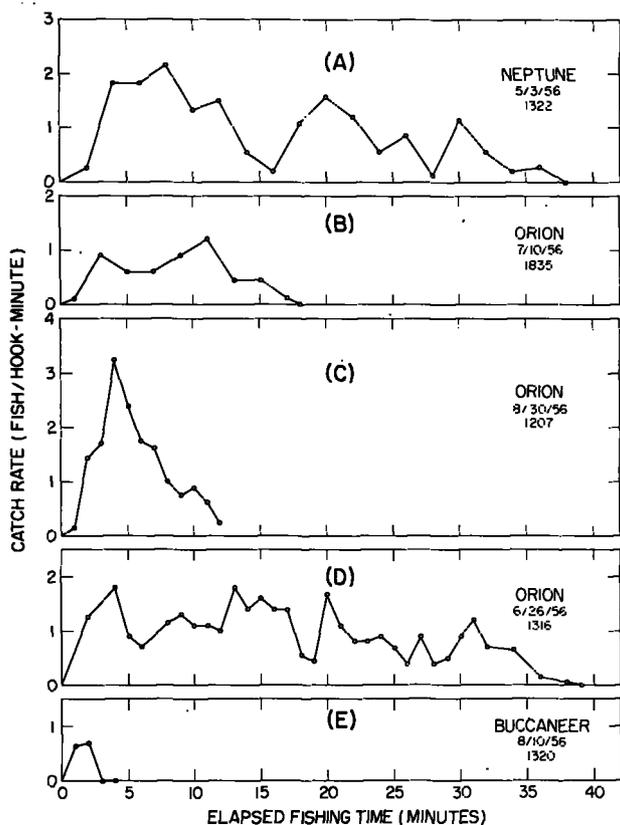


FIGURE 3.—Plots of catch rates against elapsed fishing time. A, typical. B, late peak. C, sharp decline. D, no dominant peak. E, poor response.

MEASURES OF BITING RESPONSE

Total catch per school is probably the most convenient measure of a school's response to chum. This would be the measure of most interest if it were to be applied toward estimating the fishing potential of a new area. Of the schools observed, the catch per school ranged from 1 to 773. The frequency distributions of catch per school (fig. 4) were not normal. Since the lengths of the fish fell into two distinct groups (fig. 5), the distributions were plotted separately.²

However convenient a measure the total catch may be, it is difficult to translate into terms of fish behavior because it is a reflection of a sum of behavioral and non-behavioral factors. We sought a measure of biting response that would be indicative of both behavior and yield. Correlation pro-

² Hereafter the fish will be designated as large or small depending on whether the sample means of fork lengths were more or less than 60 cm., respectively.

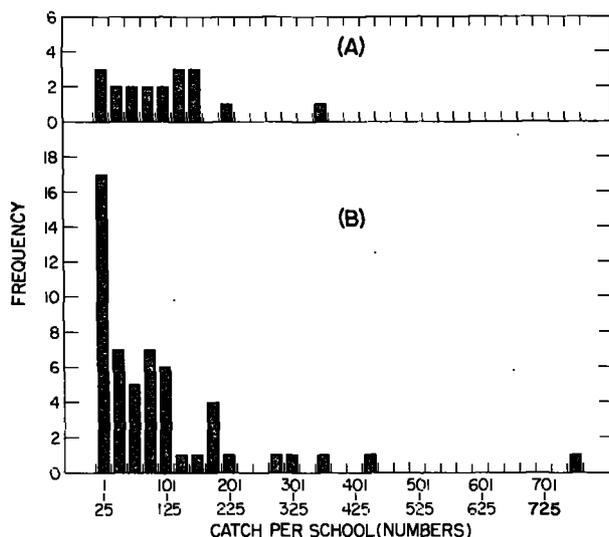


FIGURE 4.—Frequency distributions of catch per school. A, represents skipjack smaller than 60 cm. fork length. B, represents skipjack greater than 60 cm. fork length.

cedures as described by Snedecor (1946) were applied to the data to determine which of the measures of the fishing operation were associated with total catch. Since most of the frequency distributions of the various measures were skewed and sometimes truncated, Spearman's method of rank correlation was used. Computing a series of correlation coefficients is not condoned because the probability of encountering a significant correlation due to chance is increased. In this and a later section, however, such computations were included in preliminary surveys to gain information on which to base hypotheses and were not used as grounds for acceptance or rejection.

Fishing duration, which is defined as the time from the introduction of hooks into the water to their final withdrawal, was found to be highly correlated with total catch.³ The rank correlation coefficient ($r_s=0.710^{**}$) with 84 degrees of freedom is well beyond the 1-percent level of significance. (In accordance with common practice, 2 asterisks (**)) will be used to mark values beyond the 1-percent level of significance and one asterisk (*) to mark values beyond the 5-percent level.) Fishing duration ranged from 1 to 82 minutes. The frequency distributions of fishing

³ Data for this and other procedures are tabulated in the appendix, table 5.

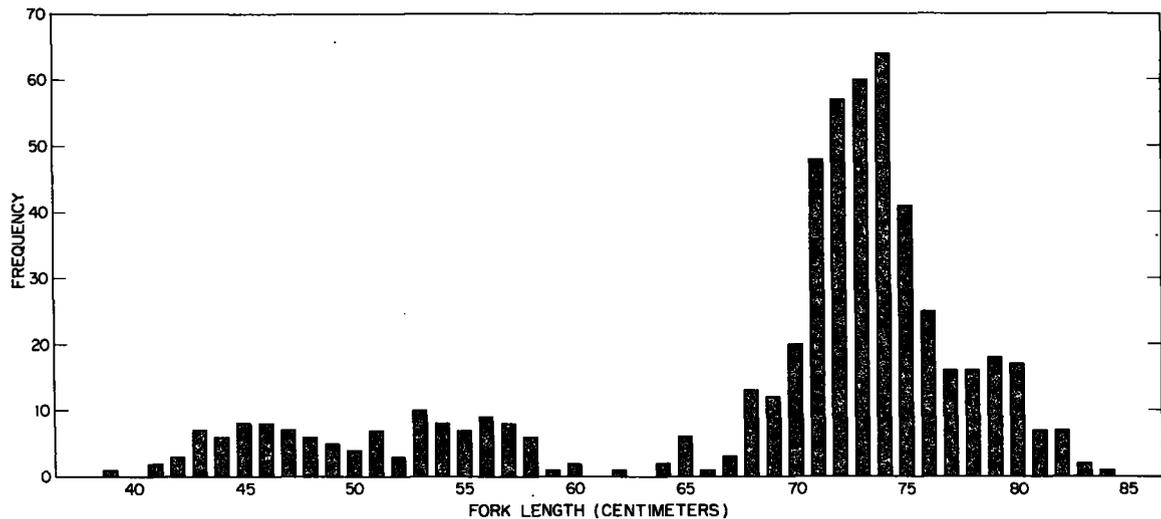


FIGURE 5.—Frequency distribution of fork lengths of skipjack sampled.

duration of small and large fish (fig. 6) does not depict any obvious difference between the two.

The peak catch rate expressed in terms of fish per hook-minute was also found to be significantly correlated with total catch ($r_s=0.796^{**}$). The range of this variate for both large and small fish is about the same. The frequency distributions of peak catch rates of large and small fish (fig. 7), however, show quite divergent modes. A dominant mode for the large fish lies somewhere between 0.40 and 1.00 fish per hook-minute, while for the small fish the mode seems to be between 3.20 and 3.40 fish per hook-minute. This

difference in peak catch rates cannot be attributed entirely to behavioral differences of the two sizes. An undetermined part of the difference is due to the greater ease with which the fishermen land the smaller fish.

The elapsed time from the start of fishing to the peak catch rate (hereafter called prepeak duration) and the time interval from the peak catch rate to the end of fishing or postpeak duration, were also compared with total catch. Post-peak duration and total catch were found to be highly correlated ($r_s=0.750^{**}$), while the prepeak duration and total catch were not ($r_s=0.204$). Prepeak duration ranged from 0.5 to 42.5 min-

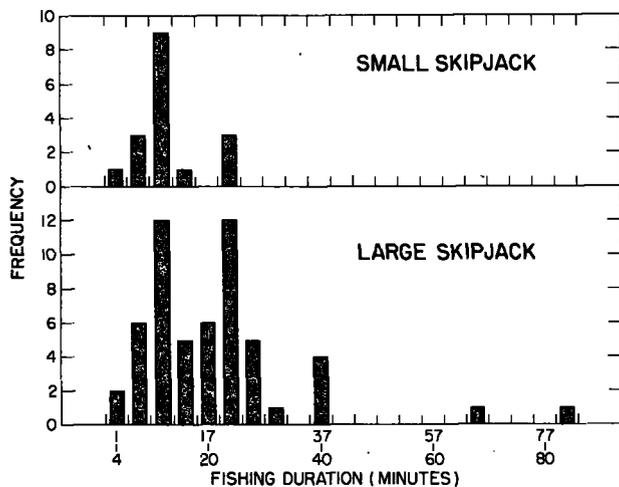


FIGURE 6.—Frequency distributions of fishing duration of large and small skipjack.

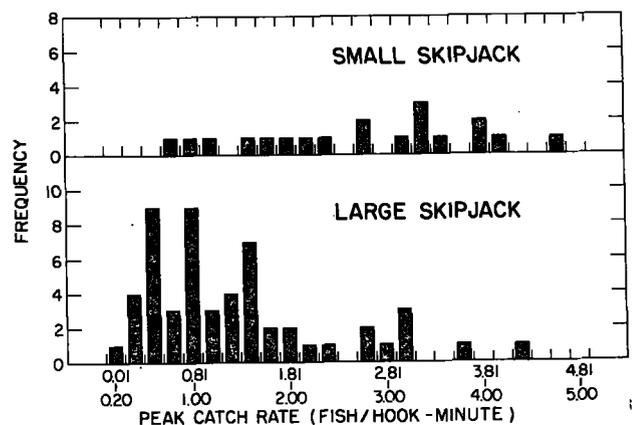


FIGURE 7.—Frequency distributions of peak catch rates for large and small skipjack.

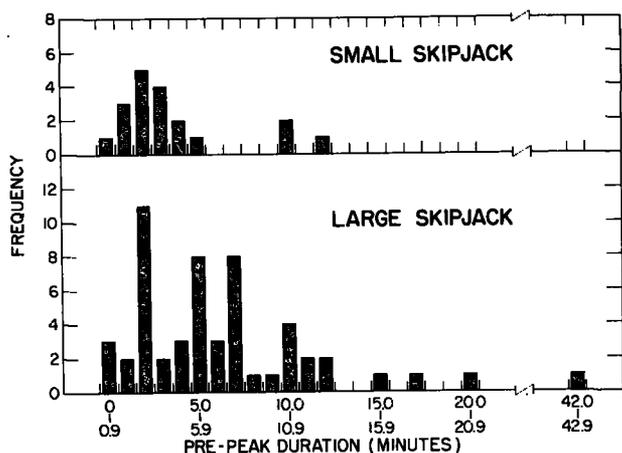


FIGURE 8.—Frequency distributions of prepeak duration for large and small skipjack.

utes (fig. 8) and postpeak duration ranged from 0 to 77 minutes (fig. 9).

The average increase per minute of the prepeak catch rates and the average decrease per minute of the postpeak catch rates for each school were computed by using regression methods with the assumption that the rates of increase and decrease were linear. The frequency distributions of these rates, placed into categories of large and small fish (fig. 10), show greater skewness in the distributions for the large fish. Total catch was found to be significantly correlated with the rate

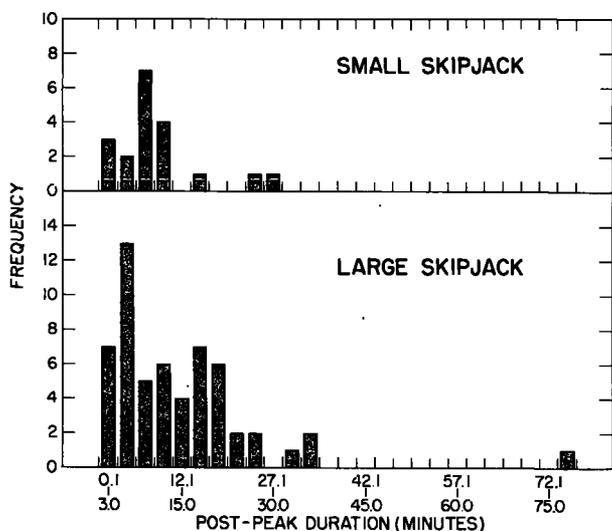


FIGURE 9.—Frequency distributions of postpeak duration for large and small skipjack.

of prepeak increase ($r_s = 0.395^{**}$) but not with the rate of postpeak decline ($r_s = -0.009$).

Another factor that affected the total catch was the mean number of hooks fished per minute. The rank correlation coefficient was 0.259^* . The grand mean number of hooks fished was 7.38 ± 1.42 .

Total catch did not seem to be influenced by the number of passes needed to stop a school (range 1 to 12 passes) nor the time interval from the start of the successful pass to the start of fishing (range of 0 to 31 minutes). The r_s values were -0.043 and 0.111 , respectively.

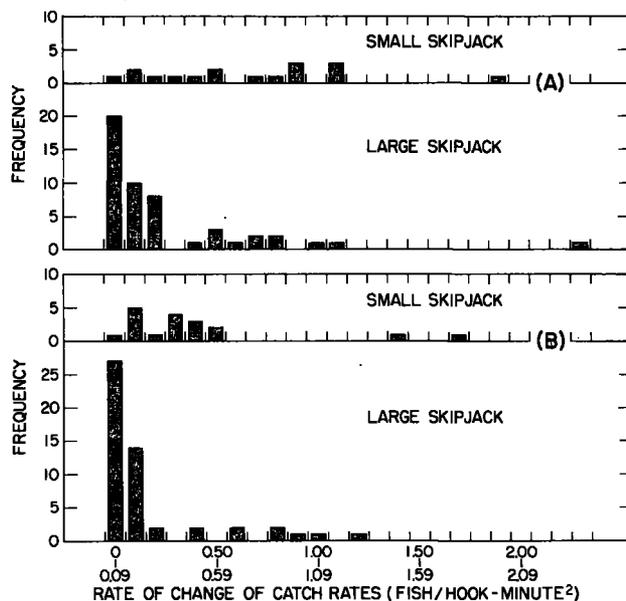


FIGURE 10.—A, Frequency distributions of rate of increase of peak catch rates. B, Frequency distributions of rate of decrease of postpeak catch rates.

Summarizing (table 1), the measured factors which seemed to influence the catch were (1) post-peak duration, (2) fishing duration, (3) peak catch rate, (4) mean number of hooks per minute, and (5) rate of increase of prepeak catch rates. Of these the peak catch rate and the postpeak duration were chosen as measures of skipjack response for use in later analyses. These, we thought, would be measures of two different aspects of response to chum. The peak catch rate would measure the degree of interest or intensity of the skipjack in feeding, and the postpeak duration would measure the duration of interest.

This by no means implies that these aspects are separate entities. In fact, the rank correlation coefficient between the two is 0.382** which may be interpreted to mean that factors common to both exist, or that one is influenced by the other.

Another consideration is that these measures may also be associated with school size. It is conceivable that a larger school would result in a longer postpeak duration. Perhaps the fish in a larger school would be more densely distributed which would result in a higher peak catch purely on a mechanical basis. It is also possible that behavior is influenced by school size. Unfortunately these possibilities must remain as conjectures for the present as no means for measuring the school size was available.

TABLE 1.—Correlation coefficients of total catch with various measures of fishing

Measure	Degrees of freedom	r
Fishing duration.....	84	0.772**
Peak catch rate.....	84	.614**
Prepeak duration.....	84	.201
Postpeak duration.....	84	.888**
Rate of prepeak increase.....	71	.274*
Rate of postpeak decrease.....	73	-.120
Mean number of hooks.....	84	.289**
Number of passes.....	81	-.06
Time from start of pass to start of fishing.....	79	.01

DESCRIPTION OF STOMACH CONTENTS

For descriptive purposes, the group designated as small fish was further divided into two groups

with 50 cm. as the separating point. The volume of the stomach contents varied markedly with fish size. The mean volume for large fish was 35.6 ml./fish. The school means ranged from 2.4 to 154.1 ml./fish. Skipjack 50 to 60 cm. in fork length showed a mean volume of 20.4 ml./fish with school means ranging from 1.5 to 55.6 ml./fish, while skipjack shorter than 50 cm. had a mean volume of 9.1 ml./fish with school means ranging from 1.3 to 15.2 ml./fish.

The food of the skipjack of the different size groups was alike and consisted of fish, mollusks, and crustaceans, but in different proportions. During the fishing season, fish accounted for 91 percent by volume of the large skipjack's diet but contributed less to the food of the smaller skipjack (fig. 11). The percentage compositions of fish in the stomachs of skipjack of 50 to 60 cm. long and skipjack less than 50 cm. long were 70 percent and 40 percent, respectively. On the other hand, mollusks and crustaceans were of relatively increasing importance with a decrease in size.

The six schools sampled during the off season, October 1956 through March 1957, produced somewhat different percentage compositions (fig. 12). Three of the schools were composed of skipjack estimated at 12 to 13 pounds and the other three consisted of skipjack estimated at 22 pounds. All of these fish would be classified as large. The percentage of fish in the stomachs was 59 percent as compared to 91 percent found during the season.

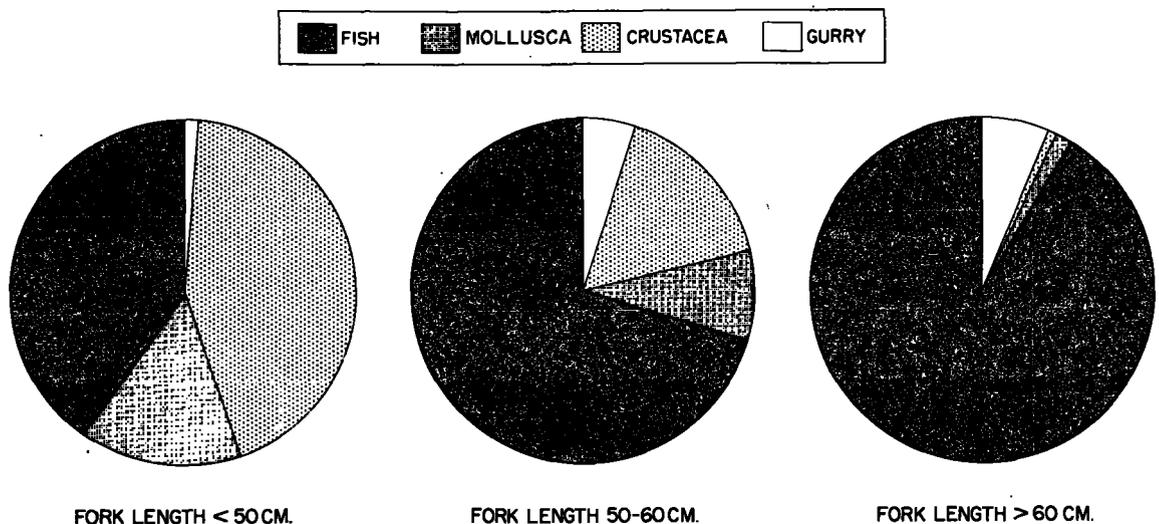


FIGURE 11.—Diagrams illustrating the composition by volume of the stomach contents of three sizes of skipjack caught during the fishing season.

Another difference between the diets of season and nonseason skipjack was the percentage of crustaceans. The figures are 36 percent for nonseason skipjack and less than 1 percent for season skipjack.

Representatives of 30 fish families and a few unidentified fish were found in the stomach contents. The families are listed in table 2 in order of percentage of total mean volume. The percentages listed are for fishes of the season and were calculated in the following manner to compensate

umes. Gurry, a small piece of wood, and a cigarette butt were classed under miscellaneous.

FACTORS INFLUENCING BITING RESPONSE

As selected in a previous section, peak catch rate and postpeak duration were used as measures of biting response. These were compared with a number of possible factors by correlation procedures or by plotting.

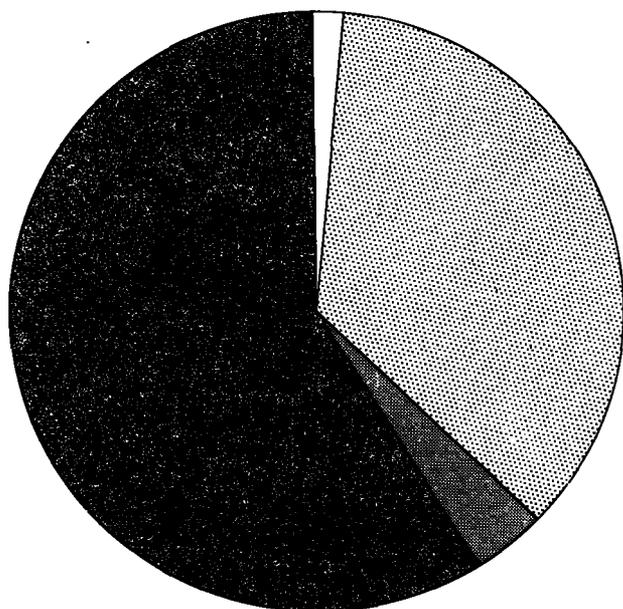
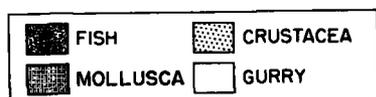


FIGURE 12.—Diagram illustrating the composition by volume of stomach contents of large skipjack caught during the off season.

for the difference in sample sizes. First, the mean volume of each category in units of ml./stomach was taken for each school. Then the total mean volume of each category was divided by the grand total mean volume and converted to percentages. In this way the contents from each school were given equal weight regardless of sample size. Carangids (genus *Decapterus*) were by far the most important item in terms of both volume and occurrence. The genus *Cubiceps* of the family Nomeidae also contributed considerably to the vol-

TABLE 2.—Stomach contents of skipjack from 34 schools

Contents		Percentage of total mean volume	Occurrence (number of schools)
Fish.....	Carangidae.....	45.01	27
	Nomeidae.....	20.25	10
	Moridae.....	6.45	6
	Thunnidae.....	3.14	13
	Gempylidae.....	2.27	19
	Sudidae.....	1.53	1
	Holocentridae.....	1.04	11
	Chaetodontidae.....	.92	21
	Bramidae.....	.59	10
	Scorpaenidae.....	.28	15
	Mullidae.....	.13	4
	Acanthuridae.....	.11	9
	Ballistidae.....	.11	7
	Sphyrnidae.....	.10	1
	Exocoetidae.....	.07	2
	Serranidae.....	.06	1
	Diodontidae.....	.05	1
	Synodontidae.....	.04	4
	Priacanthidae.....	.03	2
	Blenniidae.....	.02	3
	Ammodytidae.....	.02	3
	Fistularidae.....	.01	2
	Antigonidae.....	.01	1
Cirrhidae.....	.01	2	
Dactylopteridae.....	.01	2	
Ostraciidae.....	.01	4	
Syngnathidae.....	Trace	1	
Pomacentridae.....	Trace	1	
Tetrodontidae.....	Trace	1	
Pegasiidae.....	Trace	1	
Unidentified fish.....	.42	20	
Mollusks.....	Decapoda.....	2.28	24
	Octopoda.....	.02	1
Crustacea.....	Stomatopoda.....	2.51	24
	Decapoda.....	.94	23
	Amphipoda.....	.08	7
Miscellaneous.....	Isopoda.....	Trace	5
	Euphausiacea.....	Trace	1
		11.49	34

SKIPJACK SIZE

The mean length of the skipjack for each school was found to be significantly correlated with peak catch rate ($r_s = -0.475^{**}$). As mentioned earlier, this is at least in part attributed to the greater facility with which the small fish were landed. Correlation between mean length and postpeak duration ($r_s = -0.058$) was not significant.

HUNGER AND TIME SINCE LAST MAJOR FEEDING

The mean volume of the stomach contents (ml./stomach) for each school was used as a measure of the state of hunger. The time since the last

major feeding was expressed by the lowest stage of digestion found in the dominant fish family or families in the stomach contents of a school, using the following criteria:

- Stage 1. Fish intact.
- Stage 2. Skin or head missing.
- Stage 3. Part of flesh missing
- Stage 4. Skeletal remains.

Since the rate of digestion is not known, this measure is a relative one. Only the large skipjack caught during the season provided sufficient data for this study.

Since the stage of digestion was found to be highly correlated with the mean volume ($r_s = -0.607^{**}$), partial correlation procedures (Snedecor 1946) were used to assess the relations of these variates to biting response. Although the variates did not meet the assumption of normality, we found no other satisfactory technique and thought that these relations should be investigated.

The peak catch rate was not significantly correlated with either variate. This is in contrast to the findings of Uda (1933) and Suyehiro (1938). The former stated that skipjack with stomachs between the extremes of fullness and emptiness tended to respond more poorly to fishing when their stomachs were emptier. The latter observed that skipjack which had fed recently did not bite so well as those that were hungry. His measure of the recentness of feeding was the depth of the rugae; i.e., a smooth stomach lining indicated recent feeding. We suspect, however, that the depth of the rugae is directly related to the state of distention of the stomach, which depends upon the amount of food in it.

Multiple correlation computations of postpeak duration with stage of digestion and mean volume resulted in $R = -0.565^*$. In further computations, the partial correlation coefficient between postpeak duration and stage of digestion, independent of mean volume, was found to be -0.535^* and that between postpeak duration and mean volume, independent of stage of digestion, was found to be -0.506^* . That is to say, the postpeak duration was longer when the major items in the stomachs were in the earlier stages of digestion and the stomachs were emptier.

From this we hypothesize that live-bait fishing techniques employed in Hawaii generally do not

create a state of feeding excitement in the skipjack, but exploit an already existing one which apparently is caused by the presence of natural food. The fact that less than one-half of the schools respond to chum supports the hypothesis. Furthermore, the correlations infer that the state of excitement diminishes with feeding or with time if the skipjack were not satiated when the natural food became unavailable.

PREY BEHAVIOR

In order to determine whether any association existed between prey behavior and biting behavior of skipjack, schools were grouped according to families of fish in their stomachs. Only first and second stages of digestion were considered, and, if a school of fish had representatives of several families, the school was tabulated in each family classification. The mean peak catch rate and mean postpeak duration for each group represented by four or more schools were computed. As an example, the mean peak catch rate and the mean postpeak duration were calculated for all schools with the family Carangidae in the first and second stages of digestion.

The families are listed in tables 3 and 4 in descending order of their means. If the families were classified by their swimming abilities, the

TABLE 3.—List of fish families and peak catch rate means

Family	Mean peak catch rate (fish/hook-minute)
Nomeidae.....	1.92
Thunnidae.....	1.55
Carangidae.....	1.51
Gempylidae.....	1.47
Chaetodontidae.....	1.43
Scorpaenidae.....	1.31
Mollidae.....	1.30
Acanthuridae.....	1.17

TABLE 4.—List of fish families and postpeak duration means

Family	Postpeak duration (minutes)
Nomeidae.....	17.7
Thunnidae.....	17.5
Gempylidae.....	17.4
Scorpaenidae.....	16.4
Acanthuridae.....	15.8
Carangidae.....	15.3
Mollidae.....	14.1
Chaetodontidae.....	12.8

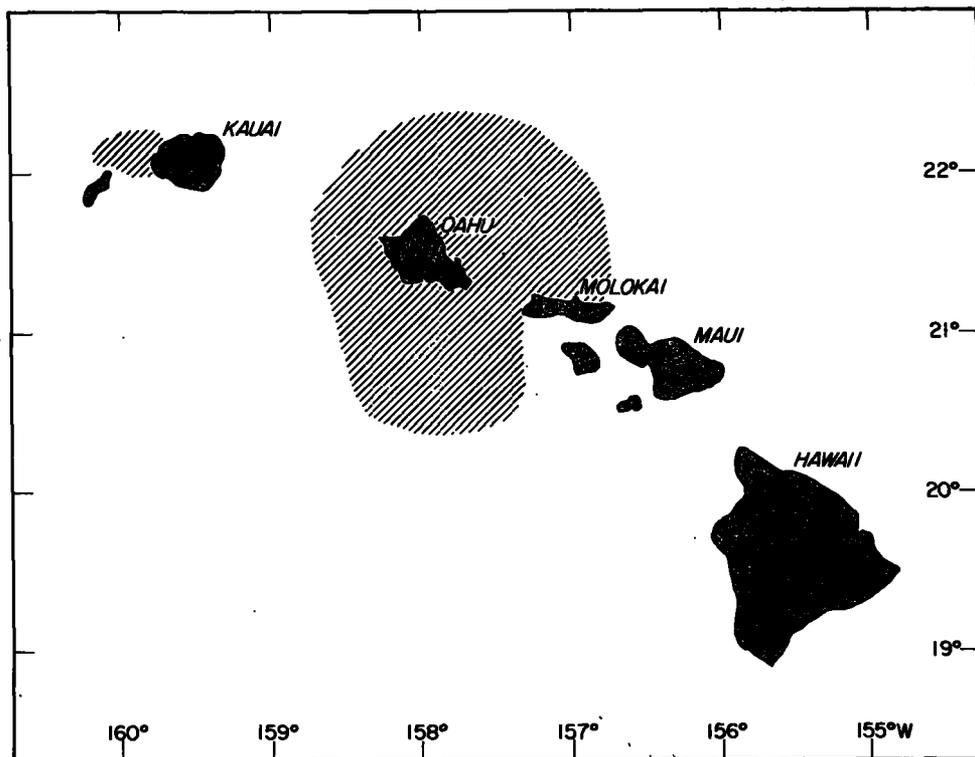


FIGURE 13.—Chart showing the areas of fishing where observations were made.

fast swimmers would include the families Thunnidae, Carangidae, Gempylidae, and Nomeidae, while the remainder would be considered slow swimmers. The fast swimmers are in the top four positions of table 3 and in the top three positions of table 4. It therefore appears that skipjack feeding on fast-swimming fish exhibit a more favorable biting behavior than skipjack feeding on slow-swimming fish.

STATE OF OVARY DEVELOPMENT

The ovaries collected from the large skipjack were all maturing. A few of the eggs were teased from the group of largest eggs in each ovary, and the diameters of five were measured. The greatest diameter found in each school was used as a rough measure of maturity. The correlations of egg diameters with peak catch rate ($r_s=0.086$) and postpeak duration ($r_s=0.258$) were not significant. The absence of ripe skipjack in the catch may be due to the reluctance of such skipjack to feed, but the stages of egg maturation other than ripeness do not appear to affect biting response.

LOCATION

All observations were made in the regions represented by the shaded areas in figure 13. The shaded area at the west end of the island of Kauai represents only one trip. The rest of the trips were within the shaded area around the island of Oahu.

The peak catch rate for large fish showed a positive significant correlation with distance from land ($r_s=0.308^*$). For small fish, the correlation was not significant ($r_s=0.057$). No significant correlation was found between postpeak duration and distance from land for either large or small fish (r_s values of -0.040 and -0.224 , respectively).

TIME OF DAY

Examination of peak catch rate, postpeak duration, and the percentage of schools successfully fished relative to time of day indicated no relation. Data on the Japanese skipjack fishery (Uda 1940a) show that catches were highest between 6 a.m. and 8 a.m., but the peak was not reflected in the catch rates. Suyehiro (1938) stated that fishing was best during early morning but provided no data.

WEATHER CONDITIONS

The weather conditions were predominantly uniform and biting behavior did not change on the unusual days. The height of the sea ranged from 1 to 10 feet, with 2 to 5 feet being the usual condition. Estimations of wind velocity ranged from 0 to 30 knots, but most of the estimates were between 10 and 20 knots. Most of the days were bright and sunny. The few darker days affected fishing only in decreasing the chances of sighting schools.

SUMMARY AND CONCLUSIONS

Commercial fishing of 92 skipjack schools was observed and resulted in the following information:

1. Fifty-two percent of the schools chummed yielded no fish.
2. The number of fish caught per school varied from 1 to 773.
3. Total fishing time per school varied from 1 to 82 minutes.
4. The number of passes required to stop a school varied from 1 to 12.
5. The mean number of hooks fished per school was 7.38 ± 1.42 .
6. Although the catch rate varied during fishing operations, the general tendency was to rise to a peak and then decline with elapsed fishing time.
7. The peak catch rate ranged from 0.12 to 4.29 fish per hook-minute for large skipjack (fork length greater than 60 cm.) with a mode of 0.40 to 1.00 fish per hook-minute, while small skipjack (fork length less than 60 cm.) had a range of 0.75 to 4.62 fish per hook-minute with a mode of 3.20 to 3.40 fish per hook-minute.
8. The prepeak duration ranged from 0.5 to 42.5 minutes with a mode of 2 to 3 minutes.
9. The postpeak duration ranged from 0 to 77 minutes with a mode of 3 to 6 minutes.
10. The catch per school was affected by fishing duration, postpeak duration (which is part of fishing duration), peak catch rate, number of hooks fished, and the rate of increase of prepeak catches.

Examination of the contents of 573 stomachs representing 49 schools revealed the following:

1. The mean volumes of stomach contents for skipjack of fork length greater than 60 cm., 50 to 60 cm., and less than 50 cm. were 35.6 ml., 20.4 ml., and 9.1 ml., respectively.

2. The percentage of fish in the stomachs collected during the fishing season decreased with a decrease in skipjack size while the percentages of mollusks and crustaceans increased.

3. The percentage of fish in the stomachs of large skipjack caught during the off season was less than that of those caught during the season. The reverse was true of the percentage of crustaceans.

4. The fish contributing most to the diet of skipjack were the genus *Decapterus*, of the family Carangidae, and the genus *Cubiceps*, of the family Nomeidae.

5. Representatives of more than 30 families of fish were found in the stomachs.

A study of the causal factors of the variation in biting response showed that—

1. Large skipjack tended to take the hooks faster the farther away they were from land.

2. The duration of response to chum was negatively correlated with mean stomach volumes and the stage of digestion of the dominant component of the stomach contents.

3. Skipjack feeding on fast-swimming fish were caught at a faster rate and fished for a longer period than those feeding on slow-swimming fish.

4. The relation between the state of ovary development and biting response is not clear, but only skipjack in the maturing stage were caught. In the maturing stage there was no correlation between biting response and a slight gradient in egg development.

5. Biting response was not affected by the time of day or weather conditions.

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APPENDIX

Data from schools fished during skipjack season

[Data from 6 schools fished in competition with other boats are not listed]

Date	Starting time	Total catch	Number of passes needed to stop school	Prepeak duration (minutes)	Postpeak duration (minutes)	Fishing duration (minutes)	Mean number of hooks fished (hooks/minute)	Peak catch rate (fish/hook-minute)	Rate of increase of pre-peak catch rates (fish/hook-minute)	Rate of decrease of post-peak catch rates (fish/hook-minute)	Distance from land (miles) ¹	Fish size ²	Mean volume of stomach contents (ml./stomach)	Lowest stage of digestion of major components	
1966															
May	3	1036	5	2	10.5	0.5	11	6.5	0.50	0.02		B			
	3	1322	280	1	7.0	31.0	38	7.9	2.17	.28	0.045	B			
	8	1453	49	1	7.0	7.0	14	7.7	.88	.10	.125	B	30 W		
	8	1614	11	1	5.0	4.0	9	7.3	.42	.27	.124	B			
	8	1630	47	1	15.0	6.0	21	6.9	.75	.03	.104	B			
	8	1805	81	7	3.0	4.0	7	8.3	2.25	.62	.689	B			
	15	0815	87	1	5.0	12.0	17	8.8	1.15	.18	.061	B	20 L		
	15	0900	66	3	5.0	16.0	21	8.1	1.06	.21	.068	B	20 L		
June	16	1538	15	1	7.0	17.0	24	7.6	.29	.02	.014	B	18 L		
	21	0845	197	1	0.5	20.5	21	9.7	3.62		.064	B	10 W		
	21	1208	47	1	1.0	13.0	14	9.1	0.75		.065	B	15 W		
	21	1412	773	1	5.0	77.0	82	9.7	3.18	.78	.031	B	20 W	18.6	
	26	1242	118	1	7.0	17.0	24	10.0	1.45	.16	.050	B	30 W	32.5	
	26	1316	385	1	3.0	36.0	39	9.9	1.80	.28	.032	B	30 W	14.1	
	26	1459	44	1	4.5	5.5	10	9.4	.89	.16	.114	B	30 W		
	26	1522	245	1	3.5	23.5	27	9.0	1.89	.50	.038	B	30 W		
	26	1629	140	1	6.0	15.0	21	6.0	2.50	.43	.139	B	25 W		
	29	1112	4	2	5.0	4.0	9	7.3	.12	.03	.034	B		154.1	
	29	1142	104	1	9.0	13.0	22	9.0	1.20	.14	.084	B			
	29	1613	110	1	7.0	18.0	25	7.8	1.50	.27	.052	B		54.3	
July	3	0910	79	2	12.0	12.0	24	7.5	1.00	.03	.041	B	10 W	41.6	
	4	1002	58	1	2.0	21.0	23	6.8	.69	.28	.019	B	10 W	41.6	
	4	1204	66	4	10.0	11.0	21	7.7	1.92	.14	.148	B	6 W	101.8	
	10	0907	54	2	2.0	16.0	18	9.0	1.22	.56	.044	B	15 W	22.6	
	10	0950	79	1	2.0	10.0	12	9.2	1.28	.59	.111	B	15 W		
	10	1002	32	1	2.0	10.0	12	8.2	.50	.18	.070	B	15 W		
	10	1116	106	3	7.0	16.0	23	8.9	1.50	.11	.089	B	6 W	9.1	
	10	1835	90	5	10.0	8.0	18	8.7	1.21	.08	.153	B	10 W		
	17	0824	4	3	6.0	.0	6	10.3	.22	.04		B	10 W		
	17	1146	244	2	12.0	27.0	39	8.4	1.56	.09	.040	B	12 W	74.0	
	19	0811	39	1	8.0	5.0	13	6.2	.92	.06	.200	B	18 L	2.4	
	19	1245	140	12	7.0	14.0	21	6.7	1.83	.02	.121	B	50 L	5.7	
	19	1352	94	1	2.0	18.0	20	6.0	1.56	.71	.064	B	60 L		
	24	1130	8	1	5.0	4.0	9	7.0	.21	.03	.065	B	10 L	37.3	
24	1721	120	7	7.0	20.0	27	6.7	1.50	.20	.040	B	5 L	30.0		
25	0916	6	4	5.0	2.0	7	6.0	.42	.14	.420	B	20 L			
25	1602	12	5	5.0	5.0	10	6.0	.50	.09	.125	B	15 L			
26	0734	23	1	11.5	5.5	17	7.8	.38	.01	.063	B	15 L			
26	0918	43	1	17.5	12.5	30	7.4	.83	.01	.038	B	10 L			
26	1248	51	1	20.5	5.5	26	7.0	.60	.01	.153	B	8 L			
27	1003	165	1	42.5	22.5	65	6.0	1.40	.00	.041	B	10 L			

See footnotes at end of table.

Data from schools fished during skipjack season—Continued

Date	Starting time	Total catch	Number of passes needed to stop school	Prepeak duration (minutes)	Postpeak duration (minutes)	Fishing duration (minutes)	Mean number of hooks fished (hooks/minute)	Peak catch rate (fish/hook-minute)	Rate of increase of pre-peak catch rates (fish/hook-minute)	Rate of decrease of post-peak catch rates (fish/hook-minute)	Distance from land (miles) ¹	Fish size ²	Mean volume of stomach contents (ml./stomach)	Lowest stage of digestion of major components	
1856															
Aug.	8	1221	30	4	2.5	9.5	12	5.6	1.67	1.17	0.171	30 L	18.6	3	
	9	0942	10	2	6.5	1.5	8	7.0	0.86	.09	.860	20 L	106.2	2	
	10	0810	35	3	2.5	4.5	7	6.9	1.83	1.16	.466	2 W	4.7		
	10	1134	21	4	1.5	5.5	7	6.4	.92		.103	34 W	1.3		
	10	1320	12	1	1.5	1.5	3	8.7	.70			50 L			
	22	1025	3	3	.5	1.5	2	7.0	.50			40 L	11.0	3	
	30	1207	123	9	3.5	8.5	12	7.8	3.25	.96	.332	30 L	15.1		
	30	1331	171	3	3.5	8.5	12	7.5	4.00	.99	.294	30 L	22.6		
	30	1407	19	1	2.5	2.5	5	7.2	1.14	.50	.570	30 L	20.7		
	30	1440	139	1	11.5	18.5	30	7.2	1.75	.05	.071	25 L			
Sept.	12	0930	113	3	2.0	4.0	6	8.8	3.06	1.03	.630	30 L	9.2	3	
	12	0956	82	2	11.5	8.5	20	6.8	1.57	.03	.115	30 L			
1857															
May	23	0750	52	2	2.5	.5	3	6.7	3.12			10 W			
	23	0832	2	1	.5	.5	1	5.0	.40			20 W			
	23	0846	13	1	1.5	.5	2	5.0	2.20			20 W			
	23	0912	17	1	1.5	.5	2	6.0	2.14			20 W			
	23	1301	22	3	2.5	5.5	8	6.9	1.00	.50	.123	30 W	4.5	3	
	23	1612	189	11	1.5	21.5	23	6.9	2.80	2.30	.109	25 W			
June	13	1207	128	1	2.5	7.0	10	6.4	3.29	.58	.382	20 W	18.2		
	19	1007	19	4	.5	8.5	9	8.6	.88		.041	10 W			
	19	1023	19	1	4.5	8.5	13	7.5	.44	.09	.038	15 W	39.7	2	
	19	1222	23	3	10.5	2.5	13	7.4	1.00	.02	1.000				
	19	1343	94	4	6.5	18.5	25	7.7	1.50	.18	.050	20 W	9.4	2	
July	3	0950	111	5	10.5	10.5	21	5.6	4.62	.30	.189	3 W	3.3		
	3	1040	356		2.5	25.5	28	7.2	4.00	1.12	.156	20 L	11.0		
	3	1207	142		2.5	9.5	12	7.2	3.55	.65	.445	20 L			
	3	1228	67	1	3.5	6.5	10	6.9	2.71	.81	.385	25 L			
	3	1317	71	1	3.5	9.5	13	7.2	1.57	.15	.113	30 L			
	3	1353	207	1	12.5	8.5	21	7.3	3.38	.02	.405	30 L			
	3	1430	83	1	4.5	6.5	11	7.7	1.62	.25	.296	30 L			
	3	1510	95	1	10.5	1.5	12	6.8	2.71	.11	1.700	30 L			
	3	1528	6	1	.5	1.5	2	5.0	.75			30 L			
	3	1552	41		1.5	10.5	12	6.6	2.12	1.12	.140	30 L			
Aug.	1	1543	188	1	2.5	16.5	19	6.9	3.00	.72	.196	40 W			
	1	1610	431	1	2.5	35.5	38	6.7	4.29	.86	.090	40 W	7.3		
	1	1747	2	2	.5	1.5	2	7.0	.29			40 W			
	1	1753	337	1	10.5	14.5	25	6.9	3.57	.21	.233	40 W			
	6	0626	157	1	4.5	27.5	32	7.9	2.33	.47	.031	1½ L			
	14	0941	84	1	2.5	16.5	19	5.8	3.00	1.50	.103	30 L	31.8		
	14	1007	15	2	2.5	12.5	15	6.5	.43	.22	.004	20 L			
	14	1806	158	1	5.5	15.5	21	6.9	3.14	.71	.172	10 L	23.5	2	
	21	1353	133	2	1.5	7.5	9	7.6	4.14	1.94	.579	55 L	55.6		
	21	1603	178	1	4.5	5.5	10	7.5	3.12	.44	.403	40 L	1.5		
	21	1706	13	4	2.5	0.5	3	5.0	1.40			40 L	214.1	1	
	21	1734	315	1	2.5	25.5	28	7.7	2.71	.86	.069	40 L			

¹ W = Windward. L = Leeward.² B = mean length > 60 cm. S = mean length < 60 cm.

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

CONTRIBUTIONS OF HUDSON AND CON- NECTICUT RIVERS TO NEW YORK-NEW JERSEY SHAD CATCH OF 1956

BY KENNETH J. FISCHLER



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ABSTRACT

Data for five meristic characters from shad sampled in 1956 in the Hudson and Connecticut Rivers were found to be representative of each shad population. These data were used to derive a calculated discriminant function which correctly classified 71.6 percent of a mixed sample of Hudson and Connecticut River shad. The percentage correctly classified was increased when the fish in the region of greatest overlap in meristic counts were not classified. Using this procedure, 79.7 percent of the fish were correctly classified and 20.3 percent were incorrectly classified.

The calculated function was applied to meristic data obtained from samples of shad taken on the New York-New Jersey coast. The proportion of shad landed on the coast classified as Hudson River or Connecticut River shad was 77 percent and 23 percent, respectively. Correcting these data for the 20.3 percent error in classification, the distribution of the 1956 coastal catch was estimated to be 90 percent Hudson River shad to 10 percent Connecticut River shad. The presence of shad in the coastal samples native to areas other than the Hudson or Connecticut Rivers was considered to be negligible. The results obtained in the meristic study compared favorably with those obtained from a tagging study which was conducted concurrently with this investigation.

CONTRIBUTIONS OF HUDSON AND CONNECTICUT RIVERS TO NEW YORK-NEW JERSEY SHAD CATCH OF 1956

By **Kenneth J. Fischler**, *Fishery Research Biologist*
BUREAU OF COMMERCIAL FISHERIES

In 1949 the Congress of the United States, acting on the request of the Atlantic States Marine Fisheries Commission, appropriated funds for the United States Fish and Wildlife Service to conduct an Atlantic coast study of the American shad (*Alosa sapidissima*). The purpose of this investigation was to determine the factors affecting the abundance of shad and to recommend measures whereby the fishery could be managed to obtain sustained yields. The shad is an anadromous fish which spends most of its life in the sea but ascends rivers in the spring to spawn. The young stay in the rivers until fall and then enter the ocean where they remain until sexually mature, 3 to 5 years later.

In this paper, meristic data are used to determine what percentage of the shad catch from the New York-New Jersey coast is native to the Hudson and Connecticut Rivers. Previous years' tagging experiments on the New York-New Jersey coast have shown that most of the shad caught here are native to the Hudson and Connecticut Rivers (Talbot and Sykes, 1958). Talbot (1954) and Fredin (1954), in their efforts to predict the size of the shad runs in the Hudson and Connecticut Rivers, concluded that yearly fluctuations in the catch of shad off the New York-New Jersey coast could affect the number of shad available to the fishery in these rivers. Thus, if regulations were adopted to increase the size of runs in these rivers and a large portion of the shad were landed on the coast, any benefits of the regulations to the river fisheries would be of limited value.

Hill (1959) postulated that it was possible to separate, with a high degree of accuracy, Hudson River shad and Connecticut River shad in a mixed sample belonging to both of these rivers by applying the method of discriminant function analysis

to the counts of certain meristic characters. Hill analyzed meristic data obtained from the Hudson River in 1939 and from the Connecticut River in 1945. In the present study, meristic data collected in the same year (1956) from both rivers were used to derive a discriminant function. This function was then used to determine the percentage of shad from the Hudson River and from the Connecticut River landed on the New York-New Jersey coast in 1956. In the analysis of data it was assumed that only shad native to the Hudson and Connecticut Rivers were present in the coastal samples. The results of this analysis were compared with those obtained from a tagging experiment (Nichols 1958) that was conducted concurrently with the meristic study.

Staff members of the U.S. Bureau of Commercial Fisheries Biological Laboratory, Beaufort, North Carolina, assisted in the study, and shad fishermen along the New York-New Jersey coast and on the Hudson and Connecticut Rivers generously supplied fish from which the meristic counts were obtained. The author is also indebted to Donald R. Hill for his review of the statistical methods used in the manuscript.

COLLECTION OF DATA

In the spring of 1956, meristic data were obtained from shad landed at three locations on the New Jersey coast and at two locations each in the Hudson River and in the Connecticut River. The two sampling locations in the Hudson River and the Rocky Hill sampling location in the Connecticut River (fig. 1) were located on shad spawning grounds. Samples from the New York-New Jersey coast were obtained over an 8-week period beginning April 1. Collections were made at Beach Haven, Point Pleasant, and Port Monmouth, N.J. Since the fish obtained at Port Monmouth were actually caught in the Staten

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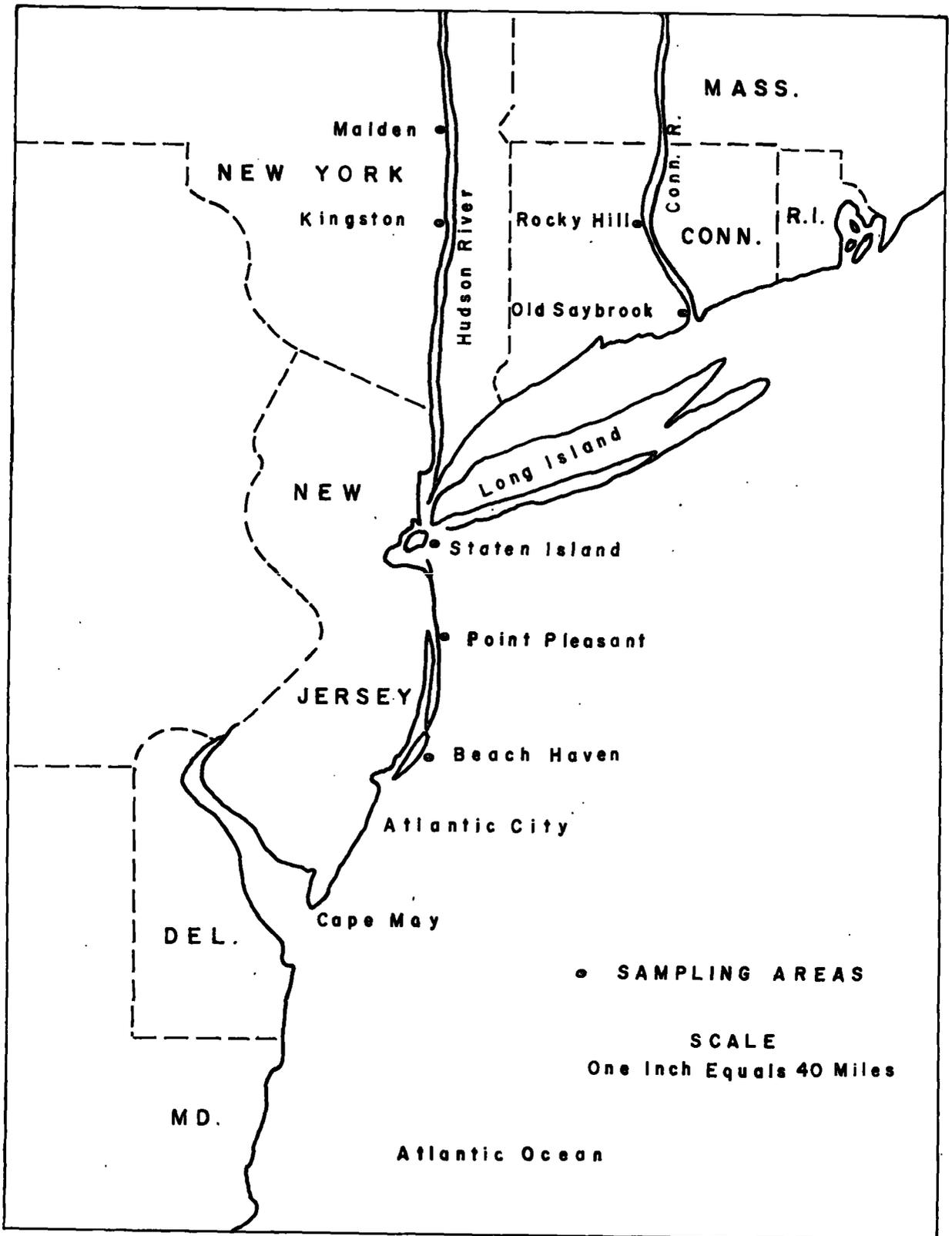


FIGURE 1.—Shad sampling areas along the New York–New Jersey coast and in the Hudson and Connecticut Rivers in 1956.

Island, N.Y., area, they will be referred to as Staten Island fish. Shad sampled at Beach Haven were taken from pound nets fished 2 miles north of Beach Haven, and the shad sampled at Point Pleasant were taken from pound nets fished 3 miles north of Point Pleasant. Samples from the Hudson River were taken weekly at Malden and Kingston, N.Y., beginning May 8 for a period of 4 weeks and at Old Saybrook and Rocky Hill, Conn., on the Connecticut River, for a 5-week period beginning May 16. Table 1 lists the number of shad sampled at each sampling location.

TABLE 1.—Number of shad (*Alosa sapidissima*) sampled, by weeks, on New York-New Jersey coast and in Hudson and Connecticut Rivers, spring 1956

Sample week	New York-New Jersey coast			Hudson River		Connecticut River		Total
	Beach Haven, N.J.	Point Pleasant, N.J.	Staten Island, N.Y.	Kingston, N.Y.	Malden, N.Y.	Old Saybrook, Conn.	Rocky Hill, Conn.	
March 31—April 6.....		20	35					55
April 7-13.....			25					25
April 14-20.....	15	20	20					55
April 21-27.....	23	20	11					54
April 28—May 4.....	30	40						70
May 5-11.....		40	30	20	20			110
May 12-18.....	8	40	24	20	20	20	20	152
May 19-25.....	9	10	10	20	20	20	20	109
May 26-June 1.....				20	20	20	20	80
June 2-8.....						20	20	40
June 9-15.....						20	20	40
Total.....	85	190	155	80	80	100	100	790

Meristic counts, fork length, weight, sex, and a scale sample were taken from each of the 790 shad studied. The age of each shad was determined from its scales using methods outlined by Cating (1953). The meristic counts were defined as follows:

Anterior scutes: All scutes from the most anterior scute just reaching the branchiostegals, counted posteriorly up to and including the scute between the ventral (pelvic) fins. The embedded portion of the last anterior scute is anterior to the origin of the ventral fins.

Posterior scutes: All scutes posterior to the ventral fins. The exposed surface of the first posterior scute in adult fish is usually longer than that of the last anterior scute.

Pectoral-fin rays: All rays in the left pectoral fin were counted.

Dorsal-fin rays: All rays including rudimentary and well-developed spinous rays (at the

anterior edge of the fin) were included in the total fin-ray count.

Anal-fin rays: Same as in the dorsal rays.

REPRESENTATIVENESS OF SAMPLES

The shad samples from the Hudson and Connecticut Rivers were taken in large-mesh gill nets (averaging 5½ inches stretch measure), and samples from the New York-New Jersey coast were taken in pound nets. Because gill nets tend to select the larger shad while pound nets are regarded as nonselective, there was a possibility that the river-sampled shad did not represent all size classes in each population, and that in their meristic count the samples taken were not representative of the exploited population in each river. To determine whether the sampled data were representative, the meristic counts were analyzed in the following manner with the results indicated:

1. Analysis of variance for linear regression of each meristic count on length in the samples obtained from each location in the Hudson and Connecticut Rivers showed no significant relation. Therefore, the counts can be regarded as varying independently of length.

2. Since none of the individual meristic counts varied significantly with length, the five meristic counts from each shad were added. These sums were used after grouping the samples by river, sex, and age group to test for any cumulative meristic variation with fish length. Of the 17 regression analyses, only one group of fish, 6-year-old males from the Hudson River, showed a significant regression (5-percent level) between total count and length. This single relation will be disregarded because significance of this nature can be expected to occur by chance in 1 of 20 similar statistical tests.

3. Analysis of variance tests, using data from all shad collected at each location in the rivers, indicated no significant differences in meristic counts between males and females of the same age group or of different age groups (4-, 5-, 6-, and 7-year-old fish).

4. There were no significant differences in total meristic count between weeks at each location, between locations, or between weeks at different locations in each river. The interaction of weeks with location was not significant in either river.

From the results obtained, it can be concluded that there was no significant relation between individual meristic counts or between total meristic counts and length. Also, no significant differences in total meristic count between the age groups in each river, between males and females of any age group, or between individual samples taken in each river were found, although the samples were obtained over a period of several weeks and at two locations in each of the rivers.

Therefore, as regards meristic counts, samples of shad taken in the Hudson and Connecticut Rivers in size-selective gill nets will be considered representative of the shad population in each river subject to exploitation by the commercial fishery and will be referred to collectively as the Hudson River sample (160 fish) and the Connecticut River sample (200 fish).

The meaning of population as used in this paper is synonymous with local population as defined by Mayr, Linsley, and Usinger (1953) as follows: "The individuals of a given locality which potentially form a single interbreeding community." A population can differ from another population in the mean values of various quantitative characters and also may differ to some degree in gene makeup or frequency.

ANALYSES OF MERISTIC DATA

To determine whether there were significant differences in meristic counts between shad from the Hudson and Connecticut Rivers, analyses of variance of the five meristic counts from samples taken in each river were calculated. These analyses are summarized in table 2. Three of the five counts showed a difference between rivers at the 1-percent level of significance and one count showed a difference at the 5-percent level. Those characters showing a difference at the 5-percent level or higher were the posterior scutes, dorsal-fin rays, pectoral-fin rays, and anal-fin rays. These four characters were of most value in separating a mixed sample of fish native to the two rivers. Linear discriminant function analysis applied to the meristic data was used to ascertain the best separation of a mixed sample of Hudson and Connecticut River shad. A simple discriminant function and a more complicated calculated discriminant function were both presented as a means of separating a mixed population. It was

shown that the calculated function distinguished Hudson from Connecticut River shad in a mixed sample with a higher degree of accuracy than the simpler function.

TABLE 2.—Analyses of variance for the five meristic characters to test for difference between rivers in 1956

(All fish (360) sampled in the Hudson and Connecticut Rivers were used in these tests)

Source of variation	df	Sum of squares	Mean square	Variance ratio <i>F</i>
Anterior scutes:				
Means.....	1	1.742	1.742	3.3
Within group.....	358	190.455	.532	
Total.....	359	192.197		
Posterior scutes:				
Means.....	1	22.894	22.894	**34.5
Within group.....	358	237.770	.664	
Total.....	359	260.664		
Dorsal-fin rays:				
Means.....	1	3.209	3.209	*5.4
Within group.....	358	212.055	.592	
Total.....	359	215.264		
Pectoral-fin rays:				
Means.....	1	23.461	23.461	**55.5
Within group.....	358	151.514	.423	
Total.....	359	174.975		
Anal-fin rays:				
Means.....	1	22.445	22.445	**24.2
Within group.....	358	332.655	.929	
Total.....	359	355.100		

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

SIMPLE DISCRIMINANT FUNCTION

Following the methods developed by Ginsburg (1938) and used by Raney and de Sylva (1953), the sum of the five meristic counts for each fish was determined for all of the shad sampled from the Hudson and Connecticut Rivers in 1956. Actually, in summing the five counts, use is made of a simple linear discriminant function, $Z = X_1 + X_2 + X_3 + X_4 + X_5$. In this function, X_1 = anterior scutes; X_2 = posterior scutes; X_3 = dorsal-fin rays; X_4 = pectoral-fin rays; X_5 = anal-fin rays; and Z = sum of the five counts. From the sums or "character indices" of all the fish in the samples, the frequency distributions of the counts from each river were tabulated (table 3).

The overall bias, or percentage of misclassification, of shad native to the Connecticut and Hudson Rivers is lowest when the distinction between the two populations is made between counts of 92 and 93. The number of shad sampled from the Connecticut River with a total count above 92 is 35, or 17.5 percent of the sample. The number of shad sampled from the Hudson River with a total count below 93 is 73, or 45.6 percent of the

TABLE 3.—Frequency distributions of simple linear discriminant function applied to meristic data from Hudson and Connecticut River shad

$$[Z = X_1 + X_2 + X_3 + X_4 + X_5]$$

Z	Connecticut River	Hudson River
84	1	
85	1	
86	3	
87	7	
88	15	2
89	16	7
90	38	8
91	39	20
92	45	36
93	14	32
94	13	28
95	8	19
96		5
97		3
Total	200	160
Mean	90.9	92.7

sample. The average percentage of shad sampled from the Connecticut River with a total count higher than 92 and of shad from the Hudson River with a total count lower than 93 is 31.5 percent. If shad with a total count above 92 are considered as being native to the Hudson River, and shad with a total count below 93 are considered as being native to the Connecticut River, the overall error of classification will be 31.5 percent. Conversely, an average of 68.5 percent of a mixed sample of Hudson and Connecticut River shad will be correctly classified. The method used to determine the percentage of shad correctly or incorrectly classified is given by Ginsburg (1938).

CALCULATED DISCRIMINANT FUNCTION

Rao (1952), Johnson (1950), and Hill (1959) show a method of finding the best linear discriminant function for two multivariate normal populations. This method gives emphasis to the large differences that occur in posterior scute counts, pectoral-fin ray counts, and anal-fin ray counts between shad from the Hudson and Connecticut Rivers, and also makes use of the smaller differences (not necessarily significant) that occur in anterior scute counts and in dorsal-fin ray counts. This discriminant function takes the form $Y = aX_1 + bX_2 + cX_3 + dX_4 + eX_5$, in which X_1 through X_5 represent the same meristic counts as previously defined, and the coefficients (a through e) are derived constants.

To obtain the discriminant function, the pooled "within group" sums of squares and sums of prod-

ucts for the meristic data from shad of the Hudson and Connecticut Rivers were divided by the number of degrees of freedom (358) which gave the variances and covariances that appear in table 4 in the form of a 5 by 5 matrix. The variances are in table 4 under $X_1 \times X_1, X_2 \times X_2, \dots, X_5 \times X_5$, and the covariances under the various combinations $X_1 \times X_2, X_1 \times X_3, \dots, X_4 \times X_5$. Following Rao (1952) and using the pivotal condensation method, the best linear discriminant function, using all five meristic characters, was obtained from the 5 by 5 matrix. The calculated function which will best discriminate between Hudson and Connecticut River shad is $Y = 0.1053X_1 + 0.8014X_2 + 0.0292X_3 + 1.1978X_4 + 0.5173X_5$. The method used to determine the discriminant function is illustrated in the appendix.

TABLE 4.—Variances and covariances of the five meristic counts in the samples of Hudson and Connecticut River shad, 1956

[Based on 360 shad]

Meristic counts	X_1	X_2	X_3	X_4	X_5	Difference in mean
X_1	0.5320	0.0060	0.0243	0.0200	0.1054	0.1400
X_2	.0060	.6642	.0235	-.0088	-.0290	.5080
X_3	.0243	.0235	.5923	.0709	.1283	.1900
X_4	.0200	-.0088	.0709	.4204	.0257	.5140
X_5	.1054	-.0290	.1283	.0257	.9292	.5030

The mean values of the meristic counts obtained in samples of shad from the Hudson and Connecticut Rivers are shown in table 5. By substituting these values into the calculated discriminant function, $Y = 0.1053X_1 + 0.8014X_2 + 0.0292X_3 + 1.1978X_4 + 0.5173X_5$, the mean Y values for shad from the Hudson (45.00) and Connecticut Rivers (43.70) are obtained. The mean Y value for the Hudson River sample is separated from the mean Y value for the Connecticut River sample by 1.30 units. This difference is also the variance of the discriminant function and is termed D^2 (Rao 1952). If D^2 is the variance of the discriminant function, the normal deviate is $\frac{D}{2}$ with mean 0 and a standard deviation of 1. The probability of obtaining a normal deviate equal to $\frac{D}{2}$ is equal to the probability that a fish from one of the two rivers will be classified correctly when the derived discriminant function is used. The probability of a normal deviate, $\frac{D}{2}$ or 0.571, is equal to 1 minus

the probability of a deviate falling outside the range of 0.571 in a 1-tailed normal distribution. This probability equals 1 minus 0.284 (Fisher and Yates, table IX, 1953) or 0.716. Thus, the calculated discriminant function will correctly classify 71.6 percent of the fish in a mixed sample of Hudson and Connecticut River shad.

TABLE 5.—Means of the five meristic counts in the samples of Hudson and Connecticut River shad, 1956

Meristic count	Hudson River ¹	Connecticut River ²
Anterior scutes, X_1	21.87	21.73
Posterior scutes, X_2	15.56	15.05
Dorsal-fin rays, X_3	18.17	17.99
Pectoral-fin rays, X_4	15.44	14.93
Anal-fin rays, X_5	21.66	21.16
Sum.....	92.7	90.9

¹ Based on 160 shad.

² Based on 200 shad.

Straight addition of the counts and the use of these "character indices" would correctly classify 68.5 percent of the shad in a mixed sample from both rivers, while the more complex calculated discriminant function will correctly classify 71.6 percent of these fish as to their native river. Rao (1952) gives a test to determine if the more complicated discriminant function is better than the simpler character-index type of function when the theoretical midpoint between the two populations is the basis of separation. Applying this test to the two functions, an F value of 7.45 was obtained, which is significant at the 1-percent level. Therefore, the calculated discriminant function was significantly better than the simpler function.

Three assumptions must be satisfied before the preceding analyses are valid: that the samples approximate multivariate normal populations; that they have equal variances and covariances; and that they are large enough to be representative of the shad population in their respective rivers. Each of the five meristic characters in the samples used in the calculations approximated normal distributions. Tests for the homogeneity of variance (Snedecor 1956) of each meristic count in shad from both rivers indicated equality. Earlier it was shown that there was no significant correlation between meristic count and length of the shad. Using methods given by Snedecor (1956), the range of the variates in the meristic samples, the estimated size of the 1956 shad population in

each river (Nichols 1958), and the tests applied, the number of fish in each sample was known to be large enough for the sample to be considered representative of each population. It was concluded, therefore, that the discriminant function was developed from sufficient data and that the samples from the two rivers were representative and did approximate multivariate normal populations with equal variances and covariances.

REDUCING ERROR IN CLASSIFICATION

The distance between the mean Y values of shad in samples from the Hudson and Connecticut Rivers after application of the calculated discriminant function is 1.30. Dividing this figure by 2 and adding the quotient to the mean for fish from the Connecticut River, the value 44.35 is obtained. All shad having a greater value than this are considered of Hudson River origin, and those below this value of Connecticut River origin. This function will classify correctly, as previously stated, 71.6 percent of the fish in a mixture of Hudson and Connecticut River shad, and incorrectly 28.4 percent. A reduction in this error of classification would be desirable.

In figure 2, two theoretical normal curves are shown representing the Y values for samples of equal size from the Connecticut and Hudson Rivers, and with the line of discrimination intersecting the line of Y values at 44.35. The error of classification (28.4 percent), using 44.35 as the separation point, is indicated by the dotted and vertical line areas. If every shad with a Y value above 45.00 is classified as a Hudson River fish, and if every shad with a Y value below 43.70 is classified as a Connecticut River fish, the maximum error of classification of fish from either the Connecticut or the Hudson River is equal to the probability of a deviate falling outside the range of the normal deviate $\frac{1.30}{1.14}$, or an error

of 12.7 percent (Fisher and Yates, table IX, 1953). This error is represented by the vertical line area in figure 2. The unclassified portion of the sample fish with their total counts, after application of the discriminant function, ranging from 43.70 to 45.00 (the dotted and cross-hatched areas of figure 2) will be an expected 37.3 percent (50 minus 12.7). Of those

fish classified (62.7 percent), $\frac{50.0}{62.7} \times 100$, or 79.7 percent will be correctly classified, and 20.3 percent will be incorrectly classified. Therefore, an increased reliability of classification has been obtained.

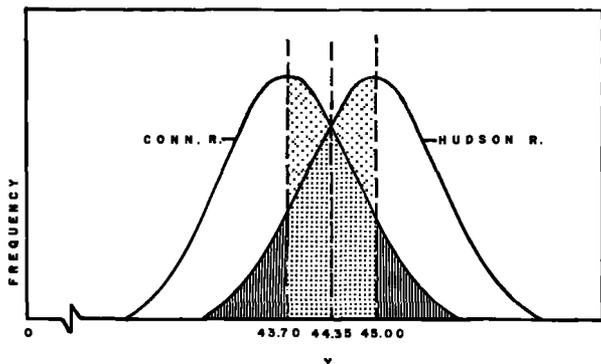


FIGURE 2.—Theoretical normal curves of the Y values for samples of shad of equal size from the Hudson and Connecticut Rivers.

APPLYING THE CALCULATED DISCRIMINANT FUNCTION

The results of applying the calculated discriminant function, $Y = 0.1053X_1 + 0.8014X_2 + 0.0292X_3 + 1.1978X_4 + 0.5173X_5$, to samples of shad from Beach Haven, Point Pleasant, and Staten Island are summarized in table 6. Those shad having a Y value above 45.00 were classified as Hudson River shad, and those having a Y value below 43.70 were classified as Connecticut River shad for a total of 265 fish. Shad with a Y value between 43.70 and 45.00 were not classified, which amounted to 165, or 38.4 percent of all the sampled shad. This is in close agreement with the expected 37.3 percent unclassified, as given in the previous section.

TABLE 6.—Classification of 265 shad from the New York-New Jersey coast as Hudson and Connecticut River fish by applying calculated discriminant function
[38.4 percent of shad in samples not classified]

Sampling location	From Hudson River		From Connecticut River		Total classified
	Number	Percent	Number	Percent	
Beach Haven.....	41	73	15	27	56
Point Pleasant.....	45	39	70	61	115
Staten Island.....	74	79	20	21	94

It was necessary to assume when applying the calculated function that the sampled shad from the New York-New Jersey coast were native to either the Hudson or Connecticut River. Therefore, the following percentages include shad correctly and incorrectly classified as from the Hudson and Connecticut Rivers and may also include shad native to other rivers along the coast. If shad native to other rivers in addition to the Hudson and Connecticut River were present in the samples obtained on the New York-New Jersey coast, an unknown bias in the percentage of Hudson River to Connecticut River shad would be introduced. This bias or error would be significant if the shad from the other rivers had a distribution of meristic counts more closely resembling those of the Hudson River than the Connecticut River, or vice versa. A further discussion of the effects of sampling shad on the New York-New Jersey coast native to neither of the two rivers will be given in a later section.

From table 6 it can be seen that 73 percent of the shad in the Beach Haven sample were classified as native to the Hudson River and 27 percent to the Connecticut River. The results at Point Pleasant were 39 percent Hudson River shad and 61 percent Connecticut River shad. At Staten Island, 79 percent of the fish in the sample were classified to the Hudson River and 21 percent to the Connecticut River. The proportion of Hudson to Connecticut River shad classified at Point Pleasant, which is located between Beach Haven and Staten Island, was almost directly opposite to that found at each of the other two stations. To determine the reason for this reversal, the best linear discriminant function for each age group was applied to the various age groups at each coastal sampling location. Although the numbers of shad in the samples differed and the meristic counts were lower in the age groups at Point Pleasant than at the other locations on the coast, the more precise Y values obtained could not account for the reversal in proportion of Hudson to Connecticut River shad in the Point Pleasant samples.

A tagging program conducted on the New Jersey coast in the spring of 1956 revealed that the shad catch from the New York-New Jersey coast was composed of 76 percent fish from the Hudson River, 13 percent from the Connecticut

River, and 11 percent from other rivers along the coast from Chesapeake Bay to the St. Lawrence River (Nichols 1958). The meristic and tagging studies gave similar results for the proportion of Hudson and Connecticut River shad in the samples obtained at Beach Haven and Staten Island, but differed in the Point Pleasant sample. Because the data obtained at Point Pleasant during the meristic study were not in agreement with those obtained at Beach Haven and Staten Island, or with those of the tagging study, it was assumed that a sampling or counting error occurred at Point Pleasant. Therefore, only the Beach Haven and Staten Island meristic data were used to estimate the proportion of Hudson and Connecticut River shad caught on the New York–New Jersey coast. Averaging the data from these two stations; the estimated percentage of shad classified to the Hudson and Connecticut Rivers that were taken off the New York–New Jersey coast in 1956 was 77 percent and 23 percent, respectively.

Discriminant function analysis will not completely discriminate a mixed sample of shad from the two rivers because 28.4 percent of the Y value distribution of each river overlaps that of the other river. Therefore, shad with Y values in the area of greatest overlap (between Y values 43.7 and 45.0 in fig. 2) were not classified. This amounted to 37.3 percent of the shad sampled in the Hudson and Connecticut Rivers, and 38.4 percent of the shad sampled on the New York–New Jersey coast. Refusing to classify 38.4 percent of all the shad sampled on the coast reduced the error in classification from 28.4 percent to 20.3 percent. This is the percentage of fish native to one river that is incorrectly classified as being native to the other river. If the coastal sample was composed of an equal number of fish from both rivers, the 20.3 percent error would cancel out. Since the percentage of shad native to the two rivers was not the same (77 percent versus 23 percent), a correction must be made to remove the 20.3 percent error and thereby obtain the best estimate of the percentage of Hudson and Connecticut River shad taken on the New York–New Jersey coast.

Of the 150 shad in the Staten Island and Beach Haven samples that were classified (table 6), 115 were classified as native to the Hudson River and 35 were classified as native to the Connecticut

River. The 115 shad classified as native to the Hudson River contained shad native to the Connecticut River, and the 35 shad classified as native to the Connecticut River contained shad native to the Hudson River. The best estimate of the number of shad native to each river was determined by solving the following pair of simultaneous equations:

$$\begin{aligned} H + 0.203 C &= 115 \\ C + 0.203 H &= 35 \end{aligned}$$

In these equations H equals the number of shad classified as Hudson River shad that were Hudson shad; $0.203 C$ equals the number of shad classified as Hudson River shad that were Connecticut River shad; C equals the number of shad classified as Connecticut River shad that were Connecticut River shad; and $0.203 H$ equals the number of shad classified as Connecticut River shad that were Hudson River shad. The number of shad sampled on the New York–New Jersey coast and assigned to the Hudson and Connecticut Rivers was 135 (112+23, or $H + 0.203 H$) and 15 (12+3, or $C + 0.203 C$), respectively. Therefore, it was concluded from this meristic study that the proportion of shad landed on the New York–New Jersey coast classified as Hudson River or Connecticut River shad was 90 percent and 10 percent, respectively.

DISCUSSION

In the analysis of meristic data, it was assumed that the catch of shad along the New York–New Jersey coast was composed only of shad native to the Hudson and Connecticut Rivers. The tagging study, which was conducted concurrently with the meristic study on the New York–New Jersey coast (Nichols 1958), revealed that 11 percent of the shad caught here in 1956 were native to streams other than the Hudson and Connecticut Rivers, from Chesapeake Bay to the St. Lawrence River. If, as estimated from tag returns, 11 percent of the shad taken on the New York–New Jersey coast were not native to the Hudson and Connecticut Rivers, there may be an error of as much as 11 percent in the proportion of shad found native to both of these rivers (90 percent Hudson, 10 percent Connecticut). The effect of shad native to other rivers on the determination of the proportion of Hudson and Connecticut River shad taken on the coast would depend on the

meristic-count distribution of these shad. If most of the fish native to other streams had total meristic counts of 45.00 and above, after application of the calculated discriminant function they would be classified as Hudson River fish; and conversely, if most of the fish had total meristic counts of 43.70 or less, they would be classified as Connecticut River fish.

Cable, in years previous to this study, collected meristic data¹ from shad caught in many shad-producing areas from Chesapeake Bay to Maine. The average meristic counts obtained by Cable for shad from areas other than the Hudson and Connecticut Rivers were generally in the range between the average 1956 counts for the shad sampled in the two rivers. Therefore, the error introduced by classifying coastal-caught shad native to other streams as Hudson River or Connecticut River fish was considered negligible.

From the tagging study which was conducted concurrently with the meristic study, it was concluded that the shad catch on the New York-New Jersey coast was composed of 76 percent Hudson River fish, 13 percent Connecticut River fish, and 11 percent fish from other areas (Nichols 1958). The proportion of Hudson River to Connecticut River fish in the New York-New Jersey coastal shad catch was determined from these data. Seventy-six percent of the shad caught on the coast were considered to be native to the Hudson River, and 13 percent were considered to be native to the Connecticut River. Consequently, the portion of Hudson River fish in a ratio of Hudson River to Connecticut River shad caught on the coast was $\frac{76}{76+13}$, or 85 percent. The portion of shad considered to be native to the Connecticut River was $\frac{13}{76+13}$, or 15 percent. Therefore, as determined from the tagging study, the best estimate of the proportion of shad landed on the coast native to the Hudson River and Connecticut River was 85 percent and 15 percent, respectively. From the meristic study it was calculated that the coastal shad catch was composed of 90 percent Hudson River and 10 percent Connecticut River fish. The proportion of shad taken on the coast native to the Hudson River and Connecticut River as deter-

mined by meristic data and tagging studies compares favorably. This favorable comparison indicates that the proportion of shad native to the Hudson River and Connecticut River taken on the coast, as calculated from the sampled meristic data, was not appreciably affected by shad native to rivers other than the Hudson and Connecticut.

In the meristic study it was assumed that the coastal catch was composed of only Hudson and Connecticut River fish; however, the tagging study revealed that approximately 11 percent of this catch was composed of shad from other areas. Since this percentage was small, its effect on the meristic determination of the proportion of Hudson River to Connecticut River shad caught on the coast would be negligible, and for practical purposes could be disregarded.

It was estimated that the cost of the meristic study was approximately one-tenth that of the tagging program. Therefore, when a meristic study is practical to separate populations, this method should be considered since it may yield information comparable to that obtained from a tagging study at only a fraction of the cost.

SUMMARY

Meristic data obtained from shad sampled on the New York-New Jersey coast and in the Hudson and Connecticut Rivers were analyzed to determine the proportion of the 1956 coastal catch native to the two rivers.

Meristic counts obtained from shad sampled in the Hudson and Connecticut Rivers were found to be representative of each shad population. Five meristic characters were used to derive a simple discriminant function that correctly classified 68.5 percent of the fish in a mixed sample of Hudson and Connecticut River shad. The calculated best linear discriminant function, which gave emphasis to the larger differences between certain meristic characters of Hudson and Connecticut River shad, correctly classified 71.6 percent of a mixed sample of Hudson and Connecticut River shad. The percentage correctly classified can be increased if the fish in the region of greatest overlap in meristic counts are not classified. Therefore, when 62.7 percent of the fish in the sample are classified, the percentage correctly classified is increased to 79.7 percent. The error in classification (20.3 percent) is the percent of

¹ Unpublished data. U.S. Bureau of Commercial Fisheries, Biological Laboratory, Beaufort, N.C.

either population classified as being native to the other population.

The calculated best linear discriminant function obtained from the Hudson and Connecticut River shad meristic data was applied to the meristic data from shad samples obtained at three locations on the New York–New Jersey coast—Beach Haven and Point Pleasant, N.J., and Staten Island, N.Y. Assuming that only shad from the Hudson and Connecticut Rivers were present in the coastal samples, the percentages of shad assigned to each river were Beach Haven, 73 percent Hudson River, 27 percent Connecticut River; Point Pleasant, 39 percent Hudson River, 61 percent Connecticut River; Staten Island, 79 percent Hudson River, 21 percent Connecticut River. The meristic data obtained at Point Pleasant were not used since they did not agree with the findings at Beach Haven or at Staten Island or with the results of the tagging program which was conducted concurrently with the meristic study.

Analysis of meristic data from shad sampled at Beach Haven and Staten Island revealed that the ratio of Hudson-to-Connecticut shad in the New York–New Jersey coast catch was 77 percent and 23 percent, respectively. After correction of these results for the 20.3 percent error in classification of shad native to either river, the percentages of Hudson and Connecticut shad in the New York–New Jersey coast shad catch in 1956 were estimated to be 90 and 10 percent.

A tagging study conducted concurrently with the meristic study on the New York–New Jersey coast revealed that the coastal shad catch was composed of 11 percent fish native to rivers other

than the Hudson and Connecticut. If these shad had meristic-count distributions similar to either Hudson or Connecticut River shad, a bias would be introduced into the determination of the proportion of Hudson to Connecticut River fish taken on the coast as determined from the meristic study. Previous studies indicate that the average meristic counts for shad caught in many shad producing areas from Maine to Chesapeake Bay are generally in the range of the meristic counts found for the shad sampled in the Hudson and Connecticut Rivers. Therefore, the error introduced into the determination of the proportion of Hudson River to Connecticut River fish in the coastal catch was considered negligible.

It was concluded from the tagging study conducted concurrently with the present investigation that the coastal shad catch was composed of 76 percent Hudson River fish, 13 percent Connecticut River fish, and 11 percent fish from other areas. The proportion of Hudson to Connecticut River shad in the coastal shad catch was therefore 85 percent and 15 percent, respectively. These results compare favorably with those obtained from the meristic study where it was determined that the coastal catch was 90 percent Hudson River fish to 10 percent Connecticut River fish.

The cost of the meristic study was approximately one-tenth that of the tagging study. Therefore, when a meristic study is practical to separate populations, it should be considered since it may yield comparable information to that obtained from a tagging study at only a fraction of the cost.

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APPENDIX

CALCULATING LINEAR DISCRIMINANT FUNCTION

Rao (1952) and Johnson (1950) outlined the method that was used to calculate the discriminant function. In this supplement, calculation of the discriminant function is presented in a simple but detailed manner. The method can be applied to any number of characters, but to simplify the process, three characters from each fish have been used. The three sets of characters from each of two groups of fish are denoted as a , b , and c . Group 1 consists of 30 fish and group 2 of 40 fish (table A-1). The steps in calculating the discriminant function are as follows:

Step 1.—Calculate the values of the characters as listed in table A-2.

TABLE A-1.—Values of three selected characters from two groups of shad

Group 1 ¹			Group 2 ²		
a_1	b_1	c_1	a_2	b_2	c_2
23	16	17	22	13	17
23	15	17	22	14	17
22	14	20	22	15	17
21	16	17	22	15	18
21	16	18	21	15	18
21	16	18	22	15	18
22	16	17	22	13	18
22	17	17	21	15	18
22	16	18	22	15	18
22	16	17	22	14	18
21	15	18	21	15	18
21	17	17	21	16	17
23	16	18	22	15	17
21	15	18	21	16	18
22	14	17	22	15	17
23	17	17	22	15	18
22	16	20	22	15	18
22	15	18	21	15	17
22	14	18	22	15	17
23	17	19	22	15	19
22	15	19	23	17	18
22	15	18	22	16	17
21	16	18	22	14	17
21	17	19	22	15	18
22	15	19	21	13	18
21	16	18	21	15	18
21	15	19	20	14	17
22	16	17	22	16	19
23	14	18	23	15	19
22	15	18	21	15	18
			21	15	19
			21	15	19
			23	13	17
			22	15	18
			22	16	18
			21	15	19
			23	15	18
			23	14	18
			21	14	19
			21	15	17

¹ Based on 30 shad.
² Based on 40 shad.

Step 2.—Calculate the pooled within-groups sums of squares and sums of products. This is shown in detail in table A-3 and summarized in table A-4.

Step 3.—The variances and covariances shown in table A-5 were determined by dividing the within-groups values in table A-4 by the number of degrees of freedom ($n_1 + n_2 - 2$), which in this case is 68. The “difference in means” column in table A-5 is determined as follows:

$$\bar{a}_1 - \bar{a}_2, \bar{b}_1 - \bar{b}_2, \text{ and } \bar{c}_1 - \bar{c}_2.$$

TABLE A-2.—Sum, mean, sum of squares, and sum of products for the three characters in the two groups of shad

Characters	Sum	Mean	Sum of squares	Sum of products
Group 1 ($n_1=30$ fish):				
a	$\Sigma a_1=656$	$\bar{a}_1=21.8667$	$\Sigma a_1^2=14,360$	$\Sigma a_1 b_1=10,232$
b	$\Sigma b_1=468$	$\bar{b}_1=15.6000$	$\Sigma b_1^2=7,326$	$\Sigma a_1 c_1=11,784$
c	$\Sigma c_1=539$	$\bar{c}_1=17.9667$	$\Sigma c_1^2=9,707$	$\Sigma b_1 c_1=8,403$
Group 2 ($n_2=40$ fish):				
a	$\Sigma a_2=868$	$\bar{a}_2=21.7000$	$\Sigma a_2^2=18,854$	$\Sigma a_2 b_2=12,869$
b	$\Sigma b_2=593$	$\bar{b}_2=14.8250$	$\Sigma b_2^2=8,821$	$\Sigma a_2 c_2=15,537$
c	$\Sigma c_2=716$	$\bar{c}_2=17.9000$	$\Sigma c_2^2=12,836$	$\Sigma b_2 c_2=10,617$

TABLE A-3.—Calculation of pooled total and group sums of squares and sums of products for groups 1 and 2

[$n_1=30$ fish; $n_2=40$ fish]

Characters	Calculation for groups 1 and 2
a_1, a_2 :	
Total.....	$\Sigma a_1^2 + \Sigma a_2^2 = 33,214.0000$
Group sums.....	$\frac{(\Sigma a_1)^2}{n_1} + \frac{(\Sigma a_2)^2}{n_2} = \frac{(656)^2}{30} + \frac{(868)^2}{40} = 33,180.1333$
a_1, b_1, a_2, b_2 :	
Total.....	$\Sigma a_1 b_1 + \Sigma a_2 b_2 = 23,101.0000$
Group sums.....	$\frac{(\Sigma a_1)(\Sigma b_1)}{n_1} + \frac{(\Sigma a_2)(\Sigma b_2)}{n_2} = \frac{(656)(468)}{30} + \frac{(868)(593)}{40} = 23,101.7000$
a_1, c_1, a_2, c_2 :	
Total.....	$\Sigma a_1 c_1 + \Sigma a_2 c_2 = 27,321.0000$
Group sums.....	$\frac{(\Sigma a_1)(\Sigma c_1)}{n_1} + \frac{(\Sigma a_2)(\Sigma c_2)}{n_2} = \frac{(656)(539)}{30} + \frac{(868)(716)}{40} = 27,323.3333$
b_1, b_2 :	
Total.....	$\Sigma b_1^2 + \Sigma b_2^2 = 16,147.0000$
Group sums.....	$\frac{(\Sigma b_1)^2}{n_1} + \frac{(\Sigma b_2)^2}{n_2} = \frac{(468)^2}{30} + \frac{(593)^2}{40} = 16,092.0250$
b_1, c_1, b_2, c_2 :	
Total.....	$\Sigma b_1 c_1 + \Sigma b_2 c_2 = 19,020.0000$
Group sums.....	$\frac{(\Sigma b_1)(\Sigma c_1)}{n_1} + \frac{(\Sigma b_2)(\Sigma c_2)}{n_2} = \frac{(468)(539)}{30} + \frac{(593)(716)}{40} = 19,023.1000$
c_1, c_2 :	
Total.....	$\Sigma c_1^2 + \Sigma c_2^2 = 22,543.0000$
Group sums.....	$\frac{(\Sigma c_1)^2}{n_1} + \frac{(\Sigma c_2)^2}{n_2} = \frac{(539)^2}{30} + \frac{(716)^2}{40} = 22,500.4333$

TABLE A-4.—Calculation of within-groups sum of squares and sum of products for the three characters within the two groups, 1 and 2

	a	b	c
a	Total=33,214.0000 Groups=33,180.1333 Within groups= 33.8667	Total=23,101.0000 Groups=23,101.7000 Within groups= -.7000	Total=27,321.0000 Groups=27,323.3333 Within groups= -2.3333
b		Total=16,147.0000 Groups=16,092.0250 Within groups= 54.9750	Total=19,020.0000 Groups=19,023.1000 Within groups= -.1000
c			Total=22,543.0000 Groups=22,500.4333 Within groups= 42.5667

TABLE A-5.—Variance and covariance based on (n₁+n₂-2) degrees of freedom

	a	b	c	Difference in means	Sum including indented
a	0.4980	-0.0103	-0.0343	0.1667	0.6201
b		.8085	-.0456	.7750	1.5276
c			.6260	.0667	.6128

TABLE A-6.—Pivotal condensation of 3 by 3 matrix to obtain successive best discriminant functions

[Numerical values]

	I	II	III	IV	V	VI
				Difference in means	Sum including indented	Check excluding indented
01	0.4980	-0.0103	-0.0343	0.1667	0.6201	
02		.8085	-.0456	.7750	1.5276	
03			.6260	.0667	.6128	
10	1.0000	-.0207	-.0689	.3347	¹ 1.0084	1.2451
11	-.0207	.8083	-.0463	.7784	1.5197	1.5404
12	-.0689		.6236	.0782	.5806	.6555
13	.3347			-.0558	1.1355	.8008
20	-.0256	1.0000	-.0573	.9630		1.8901
21	-.0701	-.0573	.6209	.1228	.6163	.6736
22	.3546	.9630		-.8054	.6350	-.3280
30	-.1129	-.0623	1.0000	.1978		.9826
31	.3685	.9743	.1978	-.8297	.7109	.5131

¹ Sum of difference.

Step 4.—Lines 01, 02, and 03 in table A-6 are the same as lines a, b, and c in table A-5. By applying the pivotal condensation method to the 3 x 3 matrix in table A-5, successive discriminant functions are obtained using one, two, and then three characters (table A-6, lines 13, 22, 31). In

table A-7, letters are used to illustrate the pivotal condensation method for obtaining the values shown in table A-6. For example, the value 0.6236 shown in line 12, column III was calculated by the formula $K - \left(G \cdot \frac{G}{E}\right)$ (table A-7, line 12, column III) as follows: 0.6260 - (-0.0343) (.0689) = 0.6236. Column VI of table A-6 is used to check on the mathematical computations as one proceeds with the pivotal condensation of the matrix.

Line 31 of table A-6 is the best linear discriminant function calculated from the three sets of measured characters. This function takes the form $Y = .3685a + .9743b + .1978c$.

CALCULATING PERCENTAGE OF MISCLASSIFICATION

If the values for \bar{a} , \bar{b} , and \bar{c} , in group 1 of table A-2 are substituted in the evolved discriminant function, the Y value for group 1 is 0.3685(21.8667) + 0.9743(15.6000) + 0.1978(17.9667) = 26.8108. When the mean Y value for group 2, 0.3685 (21.7000) + 0.9743 (14.8250) + 0.1978 (17.9000) = 25.9811, is subtracted from the Y value for group 1, the difference is 0.8297. This value is the same as line 31, column IV, table A-6, and is equal to the variance of the derived function.

TABLE A-7.—Pivotal condensation of a 3 by 3 matrix to obtain successive best discriminant functions

[Coded letter values]

	I	II	III	IV Difference in means	V Sum including indented	VI Check excluding indented
01.....	E	F	G	d_a	$(E+F+G+d_a)=L$ $(F+H+J+d_b)=M$ $(G+K+d_c)=N$ $(d_a+d_b+d_c)=T$	-----
02.....	-----	H	J	d_b		-----
03.....	-----	-----	K	d_c		-----
10.....	$\frac{E}{E}$	$\frac{F}{E}$	$\frac{G}{E}$	$\frac{d_a}{E}$	-----	$\frac{E+F+G+d_a}{E}=S$
11.....	$\frac{F}{E}$	$H - \left(\frac{F \cdot F}{E}\right) = P$	$J - \left(\frac{F \cdot G}{E}\right) = Q$	$d_b - \left(\frac{F \cdot d_a}{E}\right) = R$	Sum of line 11 = U	$M - (F \cdot S)$ or $U - \frac{F}{E}$
12.....	$\frac{G}{E}$	-----	$K - \left(\frac{G \cdot G}{E}\right) = V$	$d_c - \left(\frac{G \cdot d_a}{E}\right) = W$	Sum of line 12 + $Q = X$	$N - (G \cdot S)$ or $X - \frac{G}{E}$
13.....	$\frac{d_a}{E}$	-----	-----	$0 - \left(\frac{d_a \cdot d_a}{E}\right) = Y$	Sum of line 13 + $R + W = Z$	$T - (d_a \cdot S)$ or $Z - \frac{d_a}{E}$
20.....	$\frac{F}{E} + P = c$	$\frac{P}{P}$	$\frac{Q}{P}$	$\frac{R}{P}$	-----	$\frac{F}{E} + P + Q + R$ $\frac{\quad\quad\quad}{P} = g$
21.....	$\frac{G}{E} = (e \cdot Q) = m$	$\frac{Q}{P}$	$V - \left(\frac{Q \cdot Q}{P}\right) = h$	$W - \left(\frac{Q \cdot R}{P}\right) = j$	Sum of line 21 = f	$X - (g \cdot Q)$ or $f - \frac{Q}{P}$
22.....	$\frac{d_a}{E} = (e \cdot R) = r$	$\frac{R}{P}$	-----	$Y - \left(\frac{R \cdot R}{P}\right) = t$	Sum of line 22 + $j = z$	$Z - (G \cdot R)$ or $z - \frac{R}{P}$
30.....	$\frac{m}{h}$	$\frac{Q}{Ph} = w$	$\frac{h}{h}$	$\frac{j}{h}$	-----	Sum of line 30 = q
31.....	$r - \left(\frac{m}{h} \cdot j\right)$	$\frac{R}{P} - (w \cdot j)$	$\frac{j}{h}$	$t - \left(\frac{j \cdot j}{h}\right)$	Sum of line 31 = v	$v - \frac{j}{h}$ or $z - q \cdot j$

When 0.8297 is divided by two and this quotient (0.4148) is added to 25.9811 or subtracted from 26.8108, the value 26.3960 is obtained. If the a , b , and c values for any unclassified fish belonging to group 1 or group 2 are substituted in the discriminant function, any fish with a Y value above 26.3960 will be classified as group 1, and any fish with a Y value of less than 26.3960 will be classified as group 2.

The error of classification will be equal to 1 minus the probability of the normal deviate $\frac{0.4148}{\sqrt{0.8297}} = \frac{0.4148}{0.9110} = 0.46$. The probability of this normal deviate is 0.68 (Fisher and Yates, table IX, 1953). Therefore, the error of classification for group 1 fish or group 2 fish is 32 percent. When classifying a mixed sample containing shad belonging to either of the two groups, 32 percent of the sample will be incorrectly classified.

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

FOOD OF THE PACIFIC SARDINE (*SARDINOPS CAERULEA*)

BY CADET H. HAND AND LEO BERNER, JR.



(Contribution from Scripps Institution of Oceanography, new series)

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ABSTRACT

Stomach contents of adult and juvenile Pacific sardines (*Sardinops caerulea*), ranging in size from 31 to 285 mm. standard length, were investigated. Crustaceans were found to be the major food item, contributing 89 percent of the organic matter in the stomachs. Size of fish, within the range investigated, had little effect on the food contained in the stomachs, except for a smaller amount of phytoplankton in the juvenile fish.

A very high correlation was found between stomach contents of fish taken from a single school. The stomach contents also showed high correlation with plankton samples taken at the same time and place.

It was concluded that sardines are omnivorous, are filter feeders as well as particulate feeders, and, at least at times, are selective feeders.

FOOD OF THE PACIFIC SARDINE (*Sardinops caerulea*)

By CADET H. HAND and LEO BERNER, JR.

UNIVERSITY OF CALIFORNIA

Studies of the food of the adult Pacific sardine, *Sardinops caerulea* (Girard), have been limited in scope. Lewis (1929) studied the stomach contents of 207 sardines collected in the San Diego area and found a good relation between surface plankton and the stomach contents of these fish. He concluded that phytoplankton was a very important part of the food, although crustaceans and other zooplankters played a major role in the diet of the sardine.

Parr (1930), in a review of Lewis' data, found that zooplankton in the stomachs showed much less variation in numbers than did the phytoplankton. Using these results he suggested that zooplankters might be the object of special pursuit and the phytoplankton was ingested incidentally.

Hart and Wailes (1931) found a high proportion of diatoms in the stomachs of Canadian sardines collected in 1929, a year of very low oil production per ton of fish. The authors suggest that "red feed" (crustaceans), which makes reduction of the fish more difficult, may in the end, actually lead to higher oil production.

Radovich (1952a) examined the stomachs of 42 fish from central Baja California and southern California. He found that the bulk of the food material consisted of crustaceans, with the copepods dominating. He concluded that sardines are both filter and particulate feeders.

In 1949, the present study of the food of the adult Pacific sardine was begun as part of the Marine Life Research Program. This program is Scripps Institution's component of the California Cooperative Oceanic Fisheries Investigations, a broad study sponsored by the California Marine Research Committee and carried out cooperatively

by Scripps Institution of Oceanography of the University of California, the Bureau of Marine Fisheries of the California Department of Fish and Game, the South Pacific Fishery Investigations of the United States Fish and Wildlife Service, the Hopkins Marine Station of Stanford University, and the California Academy of Sciences.

The authors are indebted to John Radovich, California Department of Fish and Game, and to Drs. M. W. Johnson and E. W. Fager of Scripps Institution for their critical reading of the manuscript and many helpful suggestions.

METHODS

The fish from which the stomach samples were obtained were collected along the coast of central Baja California and southern California by the California Department of Fish and Game (see figs. 1 to 3 and table 3). Various methods of collection were used: gill net, beach seine, dip net, and dynamite. The majority of the specimens were collected at night by the latter method. The digestive tracts were removed immediately and preserved in formalin for transport to the laboratory. The earlier collections included digestive tracts alone; later samples were accompanied by plankton samples taken as nearly as possible at the same time and place as the fish. The plankton was collected by a net 0.5 meter in diameter, with a mesh opening of approximately 0.6 mm., hauled vertically in a standard manner. On five occasions, plankton samples were collected from various depth layers. A more complete description of the methods and of the various data taken is given by Radovich (1952b).

In the laboratory, the contents of the oesophagus and stomach, including the caecum, were removed and studied. Originally, the stomachs were analyzed separately; all items in each stomach were counted, or if the amount of material

Note.—The senior author was formerly Research Biologist, University of California, Scripps Institution of Oceanography; present address: University of California, Berkeley, California. The junior author was formerly Fishery Research Biologist, U.S. Fish and Wildlife Service, South Pacific Fishery Investigations; present address: University of California, Scripps Institution of Oceanography, La Jolla, California.

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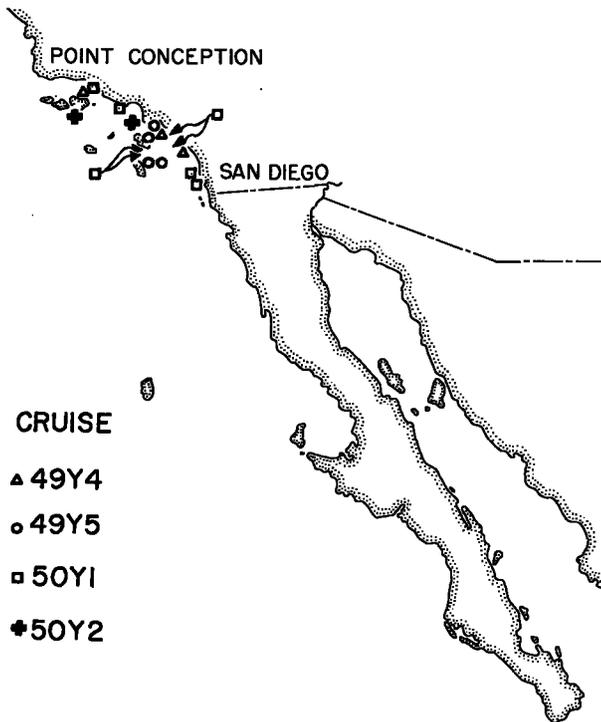


FIGURE 1.—Location of stations occupied on cruises 49Y4, 49Y5, 50Y1, and 50Y2. Arrows indicate closely spaced stations.

was too great, an aliquot of the contents was counted. After it had been established (as discussed in the next paragraph) that there was no significant variation in stomach contents between fish from the same sample (school), the stomach contents from the individual fish in each sample were combined before counting. A total of 585 stomachs was examined. Most stomachs (571) were from adult fish with standard lengths in the range 110 to 235 mm. The following discussion is based largely on these fish. The stomach contents of 14 small fish, 31 to 85 mm. standard length, were not markedly different from the adults, except for an almost complete absence of phytoplankton (appendix table 3).

In the analysis of the data on food content, it was first pertinent to establish whether or not individuals from the same school had been feeding on the same organisms. If this were found to be true, then it would not be necessary to consider each fish individually. Analysis would be facilitated by combining the stomach contents of fish from the same school. The gross appearance, texture, and color, of stomach contents of fish

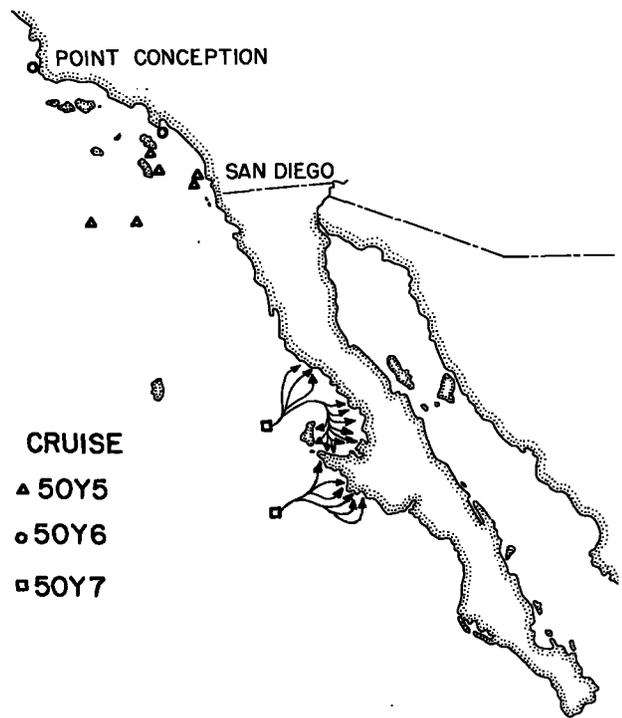


FIGURE 2.—Location of stations occupied on cruises 50Y5, 50Y6, and 50Y7. Arrows indicate closely spaced stations.

from single schools were similar and suggested that the fish had been feeding on the same organisms. The stomach contents of fish from seven samples (schools) were compared in detail. Six of the samples contained 10 fish, while the seventh contained 9. Data from a typical sample of 10 fish, 49Y5-2, are given in appendix table 1. Kendall's coefficient of concordance (Siegel 1956, pp. 229-239) was used to test for agreement among the 10 fish in regard to the relative abundances of the different organisms found in the stomachs. This method of analysis, using ranks, is distribution free. The chi-square value obtained ($\chi^2=92.6$ with 12 degrees of freedom) indicates that the probability of the agreement observed between the stomach contents of 10 fish occurring by chance alone is less than 0.001. Comparison of stomach contents within each of the other six samples indicates a similar probability for the agreement to have occurred by chance. On the basis of these data it was decided that stomach samples taken from single schools could be combined and treated as a unit.

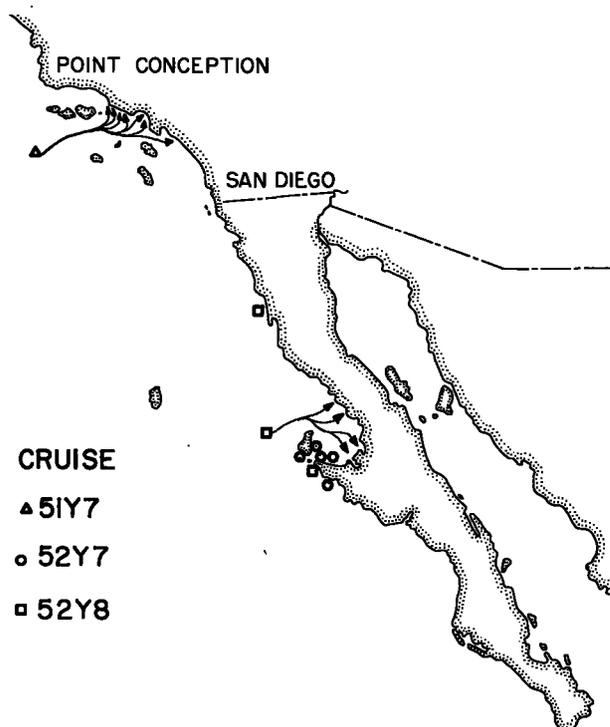


FIGURE 3.—Location of stations occupied on cruises 51Y7, 52Y7, and 52Y8. Arrows indicate closely spaced stations.

FOOD OF THE SARDINE

In all, 34 different groups of organisms were identified in the stomach contents. Owing to the semidigested condition of the material and the time involved, it was not considered practical to carry out specific identification.

The types of organisms and their percentage occurrence in the sardine stomachs are listed in table 1.

There is, in general, good agreement between the occurrence of items found in the sardine stomachs and in the plankton. Some marked differences may have resulted from the softer-bodied organisms, such as plutei, annelid larvae, doliolids, and medusae, being quickly digested in the stomachs and losing their identity, and some fast-moving animals, such as euphausiids, eluding the net. In addition, small items, such as copepod eggs and nauplii, were not properly retained by the coarse-meshed net.

Since the numbers of organisms found in the stomachs and in the plankton hauls were of different orders of magnitude, rank correlation (Kendall's tau; Siegel 1956, pp. 213-223), was used in

TABLE 1.—Frequency of occurrence of various types of organisms found in the stomachs of 273 sardines

Organism	Percentage occurrence in stomachs
Small copepods.....	100
Larvaceans.....	93
Fish eggs.....	79
Diatoms.....	75
Chaetognaths.....	73
Dinoflagellates.....	71
Large copepods.....	70
Cladocerans.....	65
Cyphonautes larvae.....	64
Euphausiid furcella and calyptopsis larvae.....	50
Gastropods (adults and larvae).....	49
Lamellibranch larvae.....	48
Copepod nauplii.....	47
Radiolarians and silicoflagellates.....	46
Euphausiid nauplii.....	40
Annelid larvae.....	36
Euphausiid eggs.....	32
Zoea larvae.....	29
Euphausiid adults.....	24
Amphipods.....	19
Barnacle nauplii.....	18
Fish larvae.....	17
Barnacle cyprids.....	16
Siphonophores.....	15
Salps.....	15
Mysids.....	13
Copepod eggs.....	10
Shrimp larvae.....	8
Brachyopod larvae.....	4
Ostracods.....	4
Foraminiferans.....	3
Doliolids.....	2
Cumaceans.....	1
Isopods.....	1

making comparisons. In every case, correlation was very good between plankton hauls in the upper layers of water and in the stomach contents. At five stations it was possible to compare stomach contents with plankton collected at various depths. As might have been expected, correlation was best between fish collected near the surface and plankton collected in the upper layers. The results of these analyses are summarized in table 2.

TABLE 2.—Comparison of contents of sardine stomachs and plankton hauls taken at the same time and place

[Basic data in appendix table 2]

Sample number	Number of items compared	Depth of haul (meters)	Rank correlation coefficient ¹
49Y5-2.....	16	(²)	+0.508 ($p=0.003$)
50Y1-16.....	13	(²)	+0.718 ($p=0.0009$)
51Y7-2.....	18	(²)	+0.302 ($p=0.038$)*
51Y7-12.....	20	(²)	+0.595 ($p=0.0001$)
50Y2-4.....	15	0-22 22-49 49-77	+0.55 ($p=0.002$) +0.33 ($p=0.041$) +0.32 ($p=0.046$)
50Y2-6.....	17	0-31 31-68 68-137	+0.552 ($p=0.001$) +0.544 ($p=0.001$) +0.353 ($p=0.023$)
50Y5-5.....	16	0-62 67-137	+0.500 ($p=0.003$) +0.416 ($p=0.012$)
50Y5-9.....	14	0-28 28-47 47-140	+0.506 ($p=0.006$) +0.363 ($p=0.034$) +0.157 ($p=0.215$)*
50Y5-13.....	11	0-62 62-140	+0.745 ($p=0.0007$) +0.411 ($p=0.039$)*

* Indicates those values in which tau values were corrected for ties.

¹ Significance level.

² From various depths; in general, from sea bottom to the surface.

TABLE 3.—List of stations with dates, times, and locations of sampling

Station	Date	Time	Location
49Y5-2.....	21-XII-49	0145	1 mile off center of Catalina Island.
50Y1-16.....	16-I-50	2225	6 miles south of Point Loma.
50Y2-4.....	28-II-50	0830	9.2 miles 323° T. from Point Vincente Light.
50Y2-6.....	1-III-50	0840	5.9 miles 038° T. from W. Point Santa Cruz Island.
50Y5-5.....	9-V-50	2140	3.5 miles off Ocean Beach.
50Y5-9.....	11-V-50	0030	60 Mile Bank.
50Y5-13.....	12-V-50	0245	32°03' x 119°48'.
51Y7-2.....	8-VIII-51	0025	2.5 miles southeast of Newport.
51Y7-12.....	11-VIII-51	2115	1 mile northeast of Point Dume.

This close correlation between stomach contents and plankton would be expected if the sardine is an omnivorous, filter-feeding fish. As stated previously, Lewis (1929) found good correlation between the sardine stomach contents he examined and plankton samples taken in the same area.

Our data do not allow any precise statement as to the degree of selection of specific food particles as opposed to the filter-feeding activities of sardines. Some stomach contents, not included in this study, indicate that sardines use both methods of feeding in nature and observations in aquariums support this view. Davies (1956) found that South African pilchards (*Sardinops ocellata*) could live as long as 6 months as particulate feeders in aquariums from which all plankton had been removed. He later concluded (1957) that the pilchard is mainly a filter feeder on plankton, but at times may be a particulate feeder. Groody (1952) observed the feeding of sardines of 200 mm. standard length in aquariums. The fish fed almost entirely by filtering. They merely oriented toward a cloud of brine shrimp, increased their swimming speed and, while the cloud was dense, did not select but plunged through it with their mouths open, filtering many shrimp from the water by the action of their gill rakers. Only when the shrimp became extremely scattered did the sardines feed on individual shrimp. During this particulate feeding, no selection of shrimp according to size was observed. Sardines accepted dead brine shrimp. This result, combined with others, led Groody to conclude that the fish found their food by reacting to odor.

Adult sardines feed selectively in nature. Samples have been examined in which the stomachs contained almost exclusively a single food item. In this investigation two particularly

unusual observations of stomach contents were noted. In one, the stomachs were filled almost entirely with euphausiids; in the other, fish larvae comprised the sole food item.

The total organic content (food value) of the more common items found in the stomachs is probably a better measure of their relative importance than either frequency or abundance alone. The organic matter contained in the following food was determined by ashing:

Organism	Size (mm.)	Average organic matter/specimen (mg.)	Number of specimens ashed
Small copepods.....	0.9	0.04	100
Large copepods.....	1.8	0.07	100
Euphausiids.....	10.0	0.9	10
Anchovy eggs.....	0.9	0.1	100
Chaetognaths.....	13.0	0.1	10

From the literature, the following values were obtained for phytoplankton organisms: Dinoflagellates (*Prorocentrum micans*), 2×10^8 cells per gram of dry material (Fox and Coe, 1943); small diatoms 6.75×10^8 cells per gram of organic matter (Fox and Coe, 1943); *Calanus finmarchicus*, 0.27 mg. per individual (Marshall, Nicholls, and Orr, 1934). Using these figures, we may estimate the nutritive role of the more prominent elements of the sardines' diet. The following results are based on average stomach contents of 571 fish:

Organism	Average number in 571 stomachs	Total organic matter (mg.)	Total organic matter (percent)
Diatoms.....	1.14×10^6	1.77	4.9
Dinoflagellates.....	33,000	0.7	1.9
Small copepods.....	666	26.64	74.2
Large copepods.....	20	3.4	9.5
Euphausiids.....	2	1.8	5.0
Chaetognaths.....	9	0.9	2.5
Fish eggs.....	7	0.7	1.9

*Average of values determined in this study and by Marshall, Nicholls, and Orr (1934).

The inclusion of the other food items found in the stomachs would not appreciably change these percentages. In the 571 stomach contents examined, small copepods, on the average, supplied about 74 percent of the total organic matter, and all crustaceans supplied nearly 89 percent. Since small copepods are so important in the diet of the sardine, a reduction in their numbers or availability might adversely affect the sardine.

The studies of Hart and Wailes (1931) indicated that the sardine in Canadian waters consumed a much higher proportion of phytoplankton. These observations were supported by the study of 68 stomach samples, collected in the fall of 1940, and supplied the authors by Dr. J. L. Hart, then director of the Pacific Biological Station, Nanaimo, B.C. (Unfortunately, the sizes of these fish were not recorded.) All of the stomachs showed a much greater phytoplankton content than any examined from the Baja or southern California area: 23 fish contained over 90 percent phytoplankton, chiefly diatoms, by volume; 36 fish more than 75 percent; 19 fish from 50 to 75 percent, and 13 fish had less than 25 percent phytoplankton. If we accept Parr's hypothesis that phytoplankton is ingested incidentally during filter feeding, the increase in diatoms in the stomachs would be expected if the numbers of diatoms increase to the north. Davies (1957) indicates an apparent preference for phytoplankton as food by the South African pilchard and suggests that the reason for congregation of schools in St. Helena Bay may be the heavy concentrations of phytoplankton in the area. He finds that phytoplankton is eaten in large quantities whenever it is available, but zooplankton is eaten mainly when phytoplankton is scarce. If this is true, Parr's hypothesis cannot be applied to the pilchard in that area.

Brodski and Jankovskaya (1935) in an investigation of the far eastern sardine, *Sardinops melanosticta*, reached much the same conclusions as Parr (1930). They concluded that the presence of diatoms in the sardine stomachs appears to be incidental to the ingestion of copepods. Further, that zooplankton (mainly copepods) is the principal food of the sardine and that phytoplankton is a so-called forced diet in the absence of zooplankton concentrations.

In our material, a comparison of organisms ingested by sardines during night and day feeding has little meaning because of the small number of samples collected during the day. On the basis of our limited data, there does not appear to be any marked difference in food organisms taken in their night and day feeding.

We found very few sardine eggs in the sardine stomachs. During cruise 52Y8, five samples containing 54 sardines in spawning condition were

collected from waters that contained sardine eggs. These fish had empty or nearly empty stomachs. In other instances where samples contained fish that were ready, or nearly ready, to spawn but where spawning had not yet occurred, nearly normal amounts of food were found in the stomachs. From these data it appears that sardines in the act of spawning or in the presence of spawning fish stop feeding. In contrast, Davies (1957) reports that the majority of fish eggs in the stomachs of South African pilchard were pilchard eggs.

SUMMARY

The stomach contents of sardines ranging in size from 31 to 285 mm. standard length were examined. Crustaceans were found to be the major food, and within that group small copepods were the most important item. In 571 fish examined, the crustaceans, on the average, contributed 89 percent of the organic matter in the stomachs; the small copepods contributed 74 percent of the total.

Owing to the lack of data on day-feeding fish, only general comparisons could be made between day and night feeding. There does not appear to be any marked difference between the two groups.

With the exception of the smaller amount of phytoplankton in the 31- to 85-mm. fish, the size of fish, within the range investigated, had little effect on the food contained in the stomachs.

Correlation between the stomach contents of fish taken from a single school was very high. The stomach contents also showed a high correlation with plankton samples taken at the same place and time. When plankton was collected from various depths, the correlation was highest in samples collected in the upper layers. These correlations give credence to the often-made statement that sardines are omnivorous, filter-feeding organisms. They do not, however, rule out particulate feeding by the fish.

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APPENDIX

APPENDIX TABLE 1.—*Stomach contents of 10 female sardines taken from one school, by length and age*

[Sample No. 49Y5-2]

Organism	Number of organisms in stomach of fish measuring—										Number found in plankton tow
	235 mm. (4 yr.)	224 mm. (3 yr.)	217 mm. (4 yr.)	224 mm. (3 yr.)	228 mm. (3 yr.)	217 mm. (4 yr.)	217 mm. (3 yr.)	222 mm. (4 yr.)	225 mm. (3 yr.)	223 mm. (3 yr.)	
Large copepods.....	30	50	4	2	15	10	40
Small copepods.....	2, 180	1, 615	16, 020	1, 005	648	1, 510	1, 490	596	740	510	2, 250
Euphausiids.....	40	15	80	10	30	25	10	15
Euphausiid calyptops larvae.....	20	30	160	15	8	25	4	10	5	40
Euphausiid furcilia larvae.....	10	40	4	10	20	2	5	20
Euphausiid nauplii.....	4	30
Euphausiid eggs.....	240	155	220	105	2	220	130	22	90	195	90
Cladocera.....	5
Cyphonautes.....	2	20
Larvaceans.....	380	145	460	145	138	350	220	148	195	380	1, 810
Chaetognaths.....	2	10	2	20	20
Fish eggs.....	3	15	12	15	10	30
Gastropods (adult and larvae).....	4	10	5	4	5	5	50
Annelid larvae.....	10

APPENDIX TABLE 2.—*Comparison of items in stomach contents of sardine samples and in plankton samples taken at same place and time, by samples*

[Absolute numbers of organisms not compared, but used only to establish rank]

Organism	Number of organisms in—							
	Sample No. 49Y5-2		Sample No. 50Y1-16		Sample No. 51Y7-2		Sample No. 51Y7-12	
	Stomach contents	Plankton sample	Stomach contents	Plankton sample	Stomach contents	Plankton sample	Stomach contents	Plankton sample
Large copepods.....	11	40	13	90	+	120	+
Small copepods.....	2, 730	2, 250	394	2, 170	340	2, 140	542	5, 270
Copepod nauplii.....	780	(*)	248	100
Euphausiids.....	23
Euphausiid calyptops larvae.....	28	40	5	10	4	40
Euphausiid furcilia larvae.....	11	+	+	10
Euphausiid nauplii.....	+	30	18	110	2	50
Euphausiid eggs.....	140	90	120
Cladocerans.....	1	9	140	+	10	8	100
Cyphonautes.....	+	20	2	40	5	30	22	140
Barnacle nauplii.....	4	30	9	30	4	90
Zoea larvae.....	2	10	+	20	+
Larvaceans.....	260	1, 810	44	120	388	1, 560	180	2, 040
Chaetognaths.....	3	20	6	60	10	30	6	140
Amphipods.....
Fish eggs.....	6	30	6	30	9	60	14	+
Gastropods.....	3	50	30	12	180
Lamellibranch larvae.....	1	30	12	40
Annelid larvae.....	10	3	60	8	10	4	30
Number of fish in sample.....	10	10	10	10
Average length of fish.....	223 mm.	192 mm.	198 mm.	208 mm.

+ Present, but average number less than 1.

* Not sampled by plankton net because of small size.

APPENDIX TABLE 2.—Comparison of items in stomach contents of sardine samples and in plankton samples taken at same place and time, by samples—Continued

Organism	Number of organisms in—						
	Sample No. 50Y5-9			Sample No. 50Y5-13			
	Stomach contents	Plankton (closing-net) sample from—			Stomach contents	Plankton (closing-net) sample from—	
		0-28 m.	28-47 m.	47-140 m.		0-62 m.	62-140 m.
Large copepods	19	130	+	35	2	20	20
Small copepods	52	1,270	190	155	16	400	90
Copepod nauplii							
Euphausiids	14	10				+	+
Euphausiid calyptopsis larvae	77	110	+		1	15	+
Euphausiid furcella larvae	40	80			2	5	+
Euphausiid nauplii				10	1	5	
Euphausiid eggs	3	30	10	5			
Cladocerans							
Cyphonautes							
Barnacle nauplii							
Zoea larvae							
Larvaceans	23	2,470	95	20	9	205	45
Chaetognaths	7	100	10	20	3	20	30
Amphipods	+	+	+			5	+
Fish eggs	+	+			26	40	
Gastropods				+			
Lamellibranch larvae							
Annelid larvae		10				5	5
Number of fish in sample	10				10		
Average length of fish	212 mm.				212 mm.		

Organism	Number of organisms in—										
	Sample No. 50Y2-4			Sample No. 50Y2-6			Sample No. 50Y5-5				
	Stomach contents	Plankton (closing-net) sample from—			Stomach contents	Plankton (closing-net) sample from—			Stomach contents	Plankton (closing-net) sample from—	
		0-22 m.	22-49 m.	49-77 m.		0-31 m.	31-68 m.	68-137 m.		0-62 m.	62-137 m.
Large copepods	9	10	5	5	20	90	75	115	672	4,260	260
Small copepods	209	228	209	257	123	1,700	875	725		20	
Copepod nauplii	8		1	1	3	120					
Euphausiids								5			
Euphausiid calyptopsis larvae	7	7	18	12		20	10			+	+
Euphausiid furcella larvae	9	4	7	34	1				48	350	40
Euphausiid nauplii									38	220	5
Euphausiid eggs					13	800	60	385		190	
Cladocerans	3	4	4		1	60		5		30	
Cyphonautes	3	2	1						12		
Barnacle nauplii											
Zoea larvae			2	1						+	5
Larvaceans					14	620	60	15			
Chaetognaths			3	6		10	30	10	24	80	30
Amphipods		3	11	10						+	5
Fish eggs	8	3	3	1					28	100	10
Gastropods		2	4	2		30	5	10		10	
Lamellibranch larvae					1		5		4	+	
Annelid larvae			3	2		10	5				
Number of fish in sample	10				4				10		
Average length of fish	207 mm.				208 mm.				190 mm.		

+ Present, but average number less than 1.

APPENDIX TABLE 3.—Stomach contents of small (less than 100 mm.) sardines

APPENDIX TABLE 3.—Stomach contents of small (less than 100 mm.) sardines—Continued

A. Sample number, 51Y8-21; time, 0200 PST; date, 30 August 1951; location, 26°58.2' N., 113°36.2' W.

C. Sample number, 50Y9-33; time, 2235 PST; date, 11 September 1950; location, 32°47.6' N., 118°24.3' W.

Organism	Number of organisms in fish measuring—			
	31 mm.	31 mm.	77 mm.	72 mm.
Small copepods.....	8	15	-----	4
Large copepods.....	-----	-----	1	3
Barnacle cypris larvae.....	-----	2	-----	-----
Zoea larvae.....	-----	-----	-----	2
Fish eggs.....	-----	-----	1	-----
Moth (Lepidoptera) ¹	-----	-----	1	-----
Diatoms.....	-----	-----	-----	(?)
Dinoflagellates.....	2	-----	-----	(?)

B. Sample number, P44-16; time, 1930 PST; date, 12 January 1953; location, 27°50.2' N., 114°50.5' W.

Organism	Number of organisms in fish measuring—				
	46 mm.	46 mm.	51 mm.	49 mm.	55 mm.
Small copepods.....	3	5	500	12	11
Large copepods.....	-----	1	4	-----	-----
Zoea larvae.....	1	1	7	1	-----
Chaetognaths.....	-----	1	-----	-----	-----
Barnacle nauplius larvae.....	-----	1	-----	-----	-----
Barnacle cypris larvae.....	1	1	-----	1	3
Lamellibranch larvae.....	-----	2	5	-----	1

Organism	Number of organisms in fish measuring—				
	49 mm.	56 mm.	71 mm.	68 mm.	85 mm.
Small copepods.....	117	9	260	190	265
Large copepods.....	12	-----	21	15	18
Cyphonautes larvae.....	14	-----	48	87	112
Barnacle cypris larvae.....	3	-----	7	2	16
Fish eggs.....	1	-----	2	1	-----
Amphipods.....	2	-----	1	-----	1
Euphausiids.....	-----	-----	3	1	2
Zoea larvae.....	-----	-----	1	-----	2
Diatoms.....	-----	-----	-----	-----	1,500
Dinoflagellates.....	-----	-----	6	+	75

+ Present, but average number less than 1.
¹ This food item cannot be considered natural, but only a very chance occurrence.
² Present in very small numbers—not counted.

APPENDIX TABLE 4.—Summary of items in stomach contents of 571 sardines and in plankton samples, by month, November 1949 to September 1952

[Asterisk (*)—specimens not properly sampled by net; NS—groups not sampled by net. Values given in each column are average number per month]

Organism	Number of organisms in—							
	Sample No. 49Y4 (Nov. 1949)		Sample Nos. 49Y4 and 49Y5 (Dec. 1949)		Sample No. 50Y1 (Jan. 1950)		Sample No. 50Y2 (Feb. 1950)	
	Stomach contents	Plankton sample ¹	Stomach contents	Plankton sample	Stomach contents	Plankton sample	Stomach contents	Plankton sample
Large copepods*	+	-----	7	36	10	27	9	10
Small copepods.....	2,900	-----	1,203	2,278	205	2,903	209	228
Copepod nauplii*	105	-----	314	15	122	78	8	-----
Copepod eggs*	1	-----	+	1	125	-----	-----	-----
Euphausiids*	7	-----	7	-----	-----	-----	-----	-----
Euphausiid calyptopsis larvae*	-----	-----	8	19	+	4	7	7
Euphausiid furellia larvae.....	+	-----	4	4	+	6	9	4
Euphausiid nauplii.....	-----	-----	+	53	+	1	-----	-----
Euphausiid eggs.....	-----	-----	40	29	+	-----	-----	-----
Cladocera.....	8	-----	3	45	-----	108	3	4
Cyphonautes.....	3	-----	4	24	9	91	3	2
Barnacle nauplii.....	1	-----	-----	-----	+	4	-----	-----
Zoea larvae.....	+	-----	-----	-----	1	2	-----	-----
Larvaceans.....	2	-----	107	818	51	450	-----	3
Chaetognaths.....	10	-----	23	23	8	29	-----	-----
Gastropods.....	2	-----	4	45	+	12	-----	2
Lamellibranch larvae.....	6	-----	2	1	-----	16	-----	-----
Fish eggs.....	+	-----	7	41	2	7	8	3
Diatoms*	1,369	-----	27,246	NS	2.6 x 10 ⁶	NS	5,330	NS
Dinoflagellates*	2,025	-----	6,739	NS	21,915	NS	-----	NS
Radiolaria and silicoflagellates*	121	-----	1,019	NS	1,540	NS	-----	NS
Average volume of food per fish.....	1.2 ml.	-----	2.1 ml.	-----	0.9 ml.	-----	0.4 ml.	-----
Number of fish.....	15	-----	38	-----	81	-----	10	-----

+ Present, but average number less than 1.
¹ No plankton collected.

APPENDIX TABLE 4.—Summary of items in stomach contents of 571 sardines and in plankton samples, by month, November 1949 to September 1952—Continued

Organism	Number of organisms in—							
	Sample No. 50Y2 (Mar. 1950)		Sample No. 50Y5 (May 1950)		Sample No. 50Y6 (June 1950)		Sample No. 50Y7 (July 1950)	
	Stomach contents	Plankton sample	Stomach contents	Plankton sample	Stomach contents	Plankton sample ¹	Stomach contents	Plankton sample ¹
Large copepods*	20	90	33	74	80	-----	42	-----
Small copepods	123	1,700	310	1,324	6,200	-----	390	-----
Copepod nauplii*	3	120	57	80	122	-----	130	-----
Copepod eggs*	-----	-----	-----	-----	-----	-----	-----	-----
Euphausiids*	-----	-----	4	3	1	-----	4	-----
Euphausiid calyptopsis larvae*	-----	-----	14	31	7	-----	11	-----
Euphausiid furellia larvae	1	20	8	18	1	-----	9	-----
Euphausiid nauplii	-----	-----	11	66	1	-----	7	-----
Euphausiid eggs	13	800	9	45	1	-----	-----	-----
Cladocera	1	60	12	33	635	-----	41	-----
Cyphonautes	-----	-----	2	5	-----	-----	7	-----
Barnacle nauplii	-----	-----	-----	-----	-----	-----	1	-----
Zoea larvae	-----	-----	-----	2	-----	-----	3	-----
Larvaceans	14	620	480	1,059	65	-----	104	-----
Chaetognaths	-----	10	16	58	5	-----	9	-----
Gastropods	-----	30	2	2	-----	-----	3	-----
Lamellibranch larvae	1	-----	1	-----	-----	-----	2	-----
Fish eggs	-----	20	-----	37	-----	-----	4	-----
Diatoms*	4.5 x 10 ⁴	NS	8.3 x 10 ⁵	NS	21 x 10 ⁴	-----	97,000	-----
Dinoflagellates*	52,000	NS	13,000	NS	6.5 x 10 ⁴	-----	27,000	-----
Radiolaria and silicoflagellates*	-----	NS	875	NS	7,000	-----	3,307	-----
Average volume of food per fish	1.0 ml.	-----	2.1 ml.	-----	1.0 ml.	-----	1.0 ml.	-----
Number of fish in sample	4	-----	63	-----	12	-----	164	-----

Organism	Number of organisms in—						Average number of organisms per fish	Average number of organisms per plankton tow	Percentage of stomachs containing organism
	Sample No. 51Y7 (Aug. 1951)		Sample No. 52Y7 (Aug. 1952)		Sample No. 52Y8 (Sept. 1952)				
	Stomach contents	Plankton sample	Stomach contents	Plankton sample ¹	Stomach contents	Plankton sample			
Large copepods*	3	102	12	-----	1	2	20	49	61
Small copepods	410	6,676	2,180	-----	167	557	666	2,238	92
Copepod nauplii*	79	15	1,180	-----	188	817	254	161	47
Copepod eggs*	-----	-----	-----	-----	-----	-----	18	NS	10
Euphausiids*	+	1	-----	-----	-----	-----	2	1	21
Euphausiid calyptopsis larvae*	2	21	-----	-----	-----	-----	6	12	33
Euphausiid furellia larvae	+	10	3	-----	-----	-----	4	9	37
Euphausiid nauplii	3	44	-----	-----	-----	-----	4	28	18
Euphausiid eggs	8	129	-----	-----	-----	-----	5	143	15
Cladocera	3	37	48	-----	68	41	39	47	53
Cyphonautes	11	105	2	-----	+	3	6	33	44
Barnacle nauplii	3	39	-----	-----	-----	-----	1	6	12
Zoea larvae	1	9	+	-----	-----	8	1	3	26
Larvaceans	111	1,792	108	-----	11	98	126	691	71
Chaetognaths	5	180	11	-----	5	73	9	53	69
Gastropods	3	100	3	-----	4	3	2	28	37
Lamellibranch larvae	2	24	6	-----	+	7	3	7	35
Fish eggs	5	21	9	-----	-----	6	7	16	51
Diatoms*	1.1 x 10 ⁴	NS	64,200	-----	71,600	NS	1.1 x 10 ⁶	NS	65
Dinoflagellates*	20,000	NS	38,000	-----	10 ⁴	NS	33,000	NS	64
Radiolaria and silicoflagellates*	223	NS	504	-----	-----	NS	544	NS	35
Average volume of food per fish	1.0 ml.	-----	0.8 ml.	-----	0.3 ml.	-----	1.1 ml.	-----	-----
Number of fish in sample	67	-----	67	-----	50	-----	-----	-----	-----

+ Present, but average number less than 1.
¹ No plankton collected.

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

DISTRIBUTION AND ABUNDANCE OF EGGS OF THE PACIFIC SARDINE, 1952-1956

BY ELBERT H. AHLSTROM



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ABSTRACT

Distribution and abundance of eggs of the Pacific sardine (*Sardinops caerulea*) are given for the years 1952 through 1956. During this period a major change occurred in distribution of sardine spawning. In 1952 and 1953 sardine spawning was mostly confined to waters off central Baja California, but in 1954 sardine spawning spread northward to waters off southern California, and this distribution continued through 1955 and 1956. Estimates of total eggs spawned during these years ranged from 136×10^{12} to 436×10^{12} eggs.

During the major spawning period (January–July off southern California and northern Baja California; January–June off central Baja California) sardine eggs were found at temperatures between 11.0° and 21.2° C. (mean, 15.2° C.); during the later spawning period (July–December off central Baja California) at temperatures between 11.3° and 27.4° C. (mean, 18.1° C.). The average temperature at which sardine eggs were found increased in a fairly uniform fashion from north to south within the spawning range during the major spawning period.

Temperatures at which sardine eggs were obtained off southern California were slightly lower in 1951–56 than in 1940 and markedly lower than in 1941.

DISTRIBUTION AND ABUNDANCE OF EGGS OF THE PACIFIC SARDINE 1952-1956

By **ELBERT H. AHLSTROM**, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

In a previous report (Ahlstrom 1954b) I discussed the distribution and abundance of egg and larval populations of the Pacific sardine (*Sardinops caerulea*) in 1950 and 1951. This report is a continuation of the record on distribution and abundance of sardine eggs for the years 1952 through 1956.

During the period covered by the present report, a major change occurred in the distribution of sardine spawning. In 1952 and 1953, spawning was mostly confined to waters off central Baja California; in 1954 through 1956, heavy and widespread sardine spawning occurred off southern California and adjacent Baja California as well as off central Baja California. This shift in a part of the spawning population was associated with a marked change in the availability of sardines to the California commercial fishery, as will be discussed later.

Investigation of the egg and larval populations of the sardine is part of a large-scale cooperative research program, the California Cooperative Oceanic Fisheries Investigations, which is sponsored by the California Marine Research Committee and carried out cooperatively by the Scripps Institution of Oceanography of the University of California, the Bureau of Marine Fisheries of the California Department of Fish and Game, the La Jolla Biological Laboratory of the U.S. Bureau of Commercial Fisheries, the Hopkins Marine Station of Stanford University, and the California Academy of Sciences. The oceanographic-biological survey program is the primary responsibility of the Scripps Institution of Oceanography and the La Jolla Biological Laboratory; the California Department of Fish and Game has participated in some cruises.

The collections were made on the following research vessels: *E. W. Scripps*, *Crest*, *Horizon*, *Paolina T.*, *Spencer F. Baird*, *Stranger*, and *Orca*, operated by the Scripps Institution of Oceanography; the *N. B. Scofield* and *Yellowfin*, operated by the California Department of Fish and Game; and the *Black Douglas*, operated by the La Jolla Biological Laboratory. I take deep pleasure in acknowledging the cooperation given by the crews of the vessels and scientific personnel of these organizations in the collection of data at sea. Most of the personnel of the La Jolla Biological Laboratory have devoted their full time to this investigation. The distribution charts were prepared by James R. Thrailkill, the graphs by Andrew M. Vrooman. Sardine egg drawings were made by George M. Mattson.

SARDINE SPAWNING SURVEYS, 1952-56

A large-scale oceanographic-biological survey program was initiated in 1949; the distribution and density of sampling stations during the first 3 years of the program were discussed by Ahlstrom (1954b). The location and number of stations occupied during 1952 through 1956 are summarized in table 1 and illustrated in figure 1. With but few exceptions, cruises were spaced at monthly intervals. During the 5 years under consideration, there were 48 regular survey cruises, 9 cruises with partial coverage, and only 3 months with no sampling at all. On each regular survey cruise there was systematic sampling of waters off California and Baja California. A minimum sampling on a regular survey cruise was obtained in the area between Point Conception, southern California and Point San Juanico, Baja California (station lines 80-137); a more extensive coverage was obtained on many cruises. Except for August 1956, there were survey cruises at monthly

NOTE.—Approved for publication, Sept. 2, 1958. Fishery Bulletin 165.

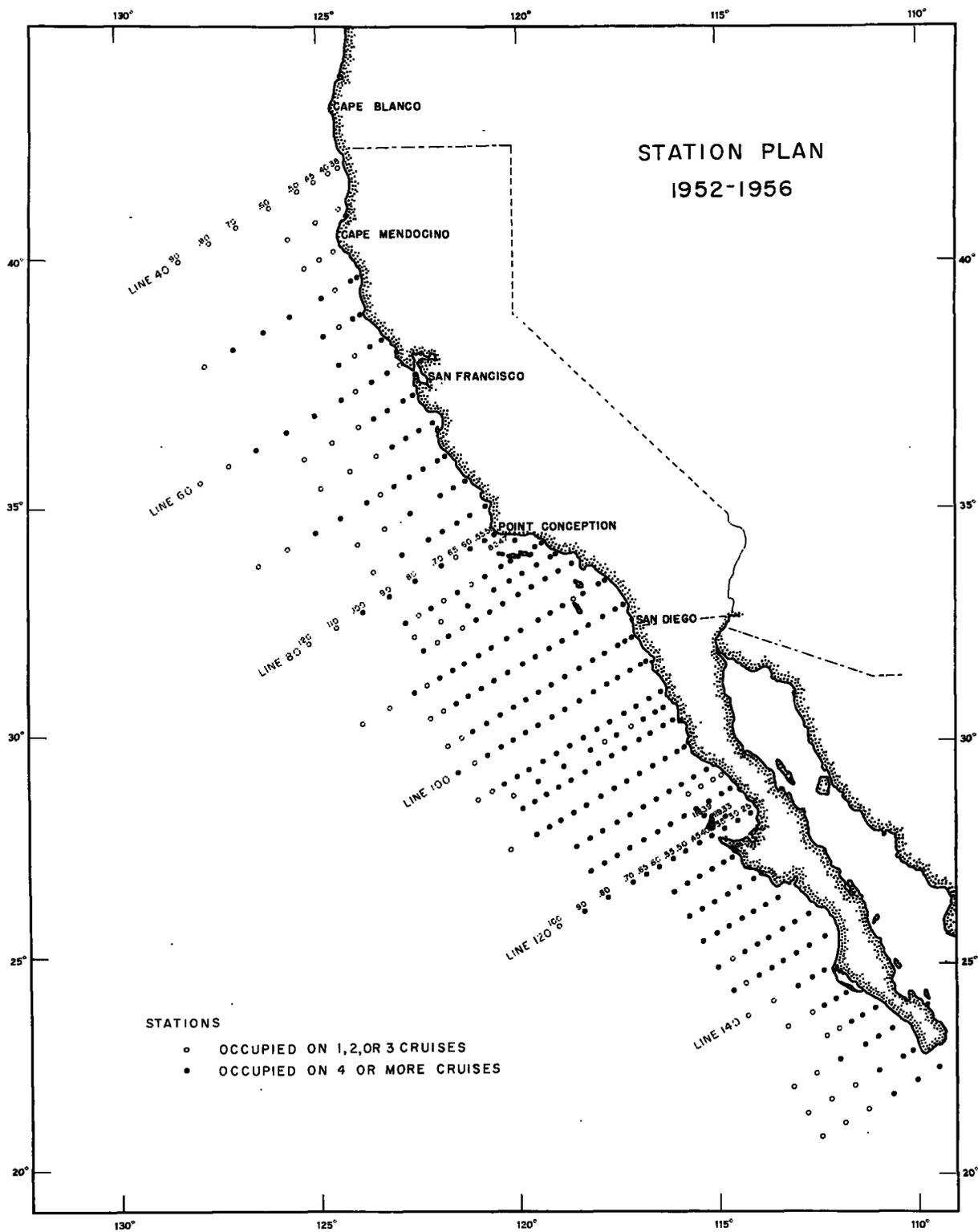


FIGURE 1.—Location of stations occupied during survey cruises made in 1952-56.

intervals during the first 8 months of each year. During the last 4 months, coverage was least extensive during September and November.

Sampling in all years was most intensive during the period of heavy sardine spawning, March

through July. After July, it was most thorough in Sebastian Viscaino Bay and in coastal waters off central Baja California, where some sardine spawning takes place throughout the latter part of the year.

TABLE 1.—Area covered and number of stations occupied on cruises of the California Cooperative Oceanic Fisheries Investigations, 1952-56

	1952		1953		1954		1955		1956	
	Area covered (lines)	Number of stations occupied	Area covered (lines)	Number of stations occupied	Area covered (lines)	Number of stations occupied	Area covered (lines)	Number of stations occupied	Area covered (lines)	Number of stations occupied
January.....	80-137	94	80-150	98	77-150	134	80-157	112	80-157	111
February.....	80-150	109	80-137	95	77-137	116	80-157	117	80-157	131
March.....	80-137	154	80-137	175	77-137	153	80-157	142	80-137	140
April.....	60-137	158	60-137	208	60-137	196	80-137	152	60-157	178
May.....	60-137	186	60-137	222	60-137	205	63-137	184	40-137	239
June.....	50-137	222	60-137	204	50-137	209	60-137	189	40-137	212
July.....	40-137	179	60-137	121	60-137	118	63-137	196	60-137	202
August.....	60-137	99	60-137	118	60-137	122	Norpac	198	110-137	36
September.....	60-137	94	83-87	40	-----	-----	83-90	169	110-137	36
October.....	60-137	88	113-120	-----	-----	-----	-----	-----	-----	-----
November.....	60-137	91	83-137	69	77-137	106	60-137	108	80-97	42
December.....	-----	-----	83-87	19	-----	-----	83-90	84	80-97	40
-----	-----	-----	83-137	82	80-157	115	80-137	106	80-97	42
Total.....	40-150	1,474	60-150	1,451	50-157	1,474	60-157	1,757	40-157	1,409

Although the total number of plankton hauls taken per year during 1952-56 was fairly similar, the temporal and areal distributions of stations were modified year by year to intensify the sampling within spawning areas at the expense of the coverage in other areas.

Detailed records were kept of each plankton haul taken during 1952 through 1956 (Staff of the South Pacific Fishery Investigations, 1953, 1954, 1955, 1956; Thraillkill 1957). Included in the record for each haul were position, date and time of occupancy, volume of water strained, depth of stratum through which the net was hauled, and volume of plankton obtained.

ESTIMATING ABUNDANCE OF SARDINE EGGS

Methods of estimating abundance of pelagic fish eggs were described by Sette and Ahlstrom (1948) and Ahlstrom (1954b). An estimate of the number of sardine eggs spawned during each cruise (C) is obtained from

$$C = \sum_i (c_i w_i t_i)$$

in which c_i = an estimate of the number of sardine eggs spawned per day in a standard area representing 10 square meters of sea surface at the i -th station, derived by dividing the total number of sardine eggs in a standard haul by the total

number of age categories represented—this is equivalent to c_{ig} , as defined in Ahlstrom (1954b); w_i = the weighting factor for space, in standard areas, that is proportional to the area of the polygon at the i -th station bounded by constructing perpendicular bisectors to lines drawn from that station to each of the adjacent stations; and t_i = the time weighting given to the i -th station, equal to one-half the time elapsed since the preceding occupancy plus one-half the time elapsed prior to the succeeding occupancy.¹

The estimated number of eggs spawned within the survey area during the year is obtained by summing C for all cruises.

Sardine eggs require from 1 to 5 days (usually 2 to 4) to develop from spawning to hatching, depending upon the temperature of the water during incubation. Sardine spawning takes place mostly during a 4-hour period, 8 p.m. to midnight (Ahlstrom 1943). Because successive spawning periods are separated by about 20 hours, eggs of the current night's spawning are sharply separated in stage of development from those spawned on the preceding night or nights. Eggs obtained from two fairly typical samples are illustrated in figure 2. Each contained eggs spawned on three consecutive nights. The tem-

¹ The time weighting given to the i -th station approximated 30 days. When coverage of a station was not obtained on successive months, an arbitrary time weighting of 30 days was allowed.

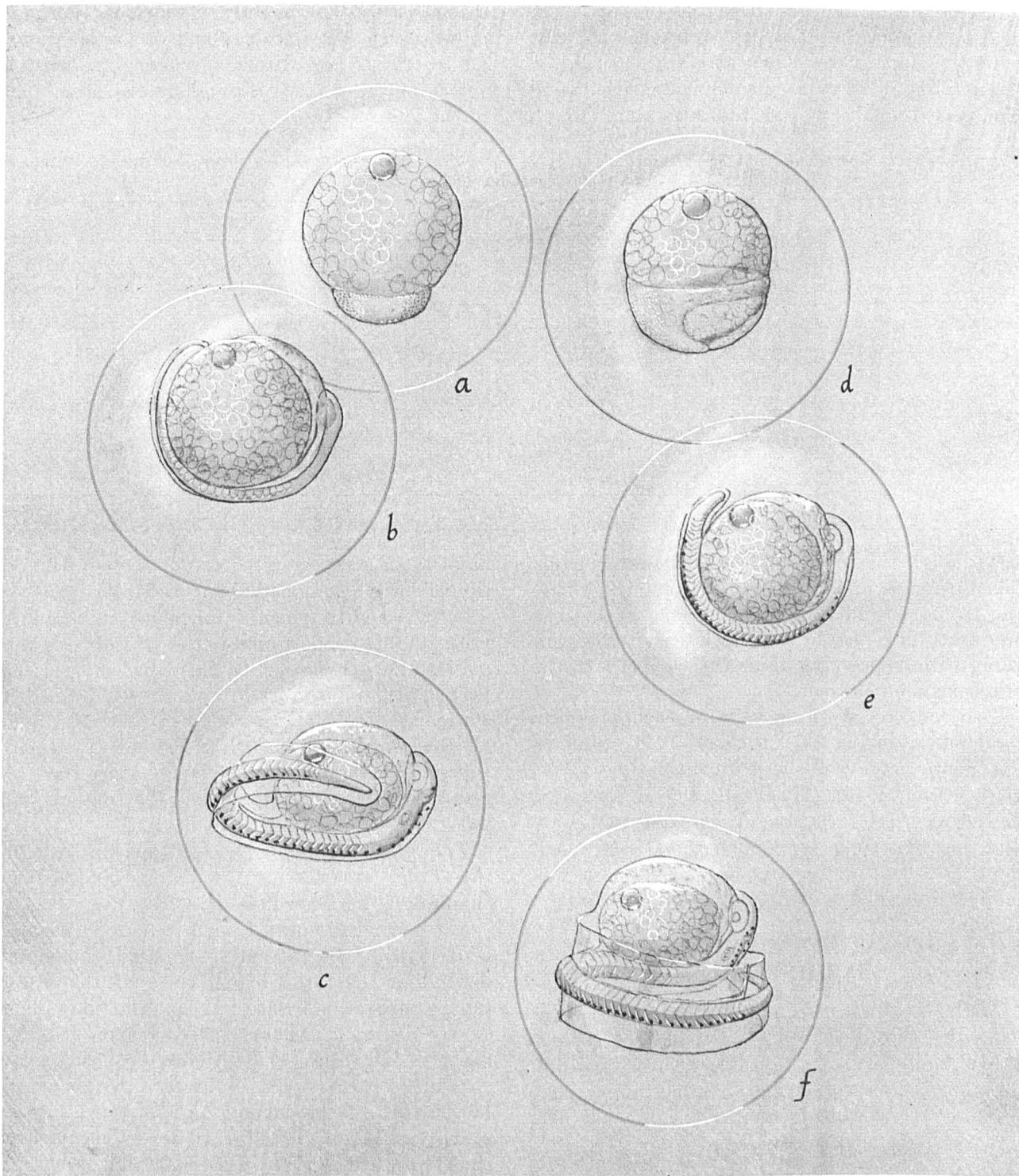


FIGURE 2.—Sardine eggs of different stages of development: a–c, the three stages of development present in a sample collected at 6 a.m. (water temperature 15.5° C.); d–f, the three stages of development present in a sample collected at 2 p.m. (water temperature 15.5° C.). The approximate age of each stage (time from spawning) is as follows: a, 8 hours; b, 32 hours; c, 56 hours; d, 16 hours; e, 40 hours; and f, 64 hours.

perature in each instance was similar (15.5° C.), but the times of collection were different—6 a.m. for the group of eggs on the left, 2 p.m. for the group on the right.

In the previous report (Ahlstrom 1954b, table 7), three estimates of the number of sardine eggs were given for 1950 and 1951, based on three different methods of determining c_i , the average number of eggs spawned per day. One method made use of the relation between water temperature and the rate of development of sardine eggs for estimating the number of days' spawning represented in a sample; a second method made use of "aged" eggs, but limited acceptable observations to complete age categories; the third made use of all age categories, except newly spawned eggs collected between 8 p.m. and midnight.

As noted in the formulation above, the third method is employed in this report. It is by far the simplest of the three methods of determining the average number of eggs spawned per day, it is more precise for individual stations than the method employing the relation between water temperature and rate of development, and it has fewer limitations than estimates based on complete age categories (see Ahlstrom 1954b: 99).

Estimates of abundance, making use of all age categories except newly spawned eggs from hauls made between 8 p.m. and midnight in determinations of per day spawning, are slightly lower, however, than estimates derived from the other methods of determining c_i . Obviously, this is because the oldest age category, in some instances, has been reduced by the hatching of some of the eggs. In 1950, for example, estimates based on all age categories were 95.2 percent as high as those based on complete age categories; in 1951 they were 97.8 percent as high, and in 1952, 98.5 percent as high.

The basic data on sardine eggs have been given in the following reports: For 1952, in Ahlstrom (1954a); 1953, in Ahlstrom and Kramer (1955); 1954, in Ahlstrom and Kramer (1956); 1955, in Ahlstrom and Kramer (1957); and 1956, in Ahlstrom (1958). In these reports, sardine eggs are enumerated by age for each collection.

DISTRIBUTION AND ABUNDANCE OF SARDINE EGGS IN 1952

The distribution of sardine eggs in 1952 is illustrated in figure 3. This chart shows relative

abundance of eggs; the concentration at each station is the cumulative standard haul total for the year.

The estimated abundance of sardine eggs in 1952 is summarized by month and station line in table 2. This table is comparable to tables 8 and 9 in the previous report (Ahlstrom 1954b). Sub-totals are given for six areas, delimited as follows:

1. Area north of Point Conception: northern and central California, station lines 40 to 77.
2. Southern California area: from Point Conception to San Diego, station lines 80 to 93.
3. Northern Baja California area: from the International Border to Point San Quintin, station lines 97-107.
4. Upper central Baja California area: from Point Baja to Point San Eugenio, station lines 110-120.
5. Lower central Baja California area: from off Turtle Bay to Point San Juanico, station lines 123-137.
6. Southern Baja California area: from Cape San Lazaro to Cape San Lucas, station lines 140-157.

In 1952, there were 11 monthly cruises (none in December), and in March, a second survey of the area off central Baja California. The estimate of the number of sardine eggs spawned in 1952 is the lowest for the 7-year period, 1950-56.

Two major sardine spawning centers were pointed out by Ahlstrom (1954b), one off southern California and northern Baja California (station lines 80-107), the other off central Baja California (station lines 110-137). The upper or northern spawning center was made up of areas 2 (southern California area) and 3 (northern Baja California area) in the above grouping of areas, while the lower or southern spawning center was made up of areas 4 and 5, off central Baja California. The separation of the two centers was most complete in 1951 (Ahlstrom 1954b, fig. 8). This separation was again apparent in 1952 and 1957. The latter is not included in the present report. In intervening years, however, the separation has been less complete, and in 1954, 1955, and 1956, spawning was continuous between the two areas. It is convenient, however, to retain the geographic separation of spawning into two primary centers, or areas, especially since there has been such a marked change in the distribution

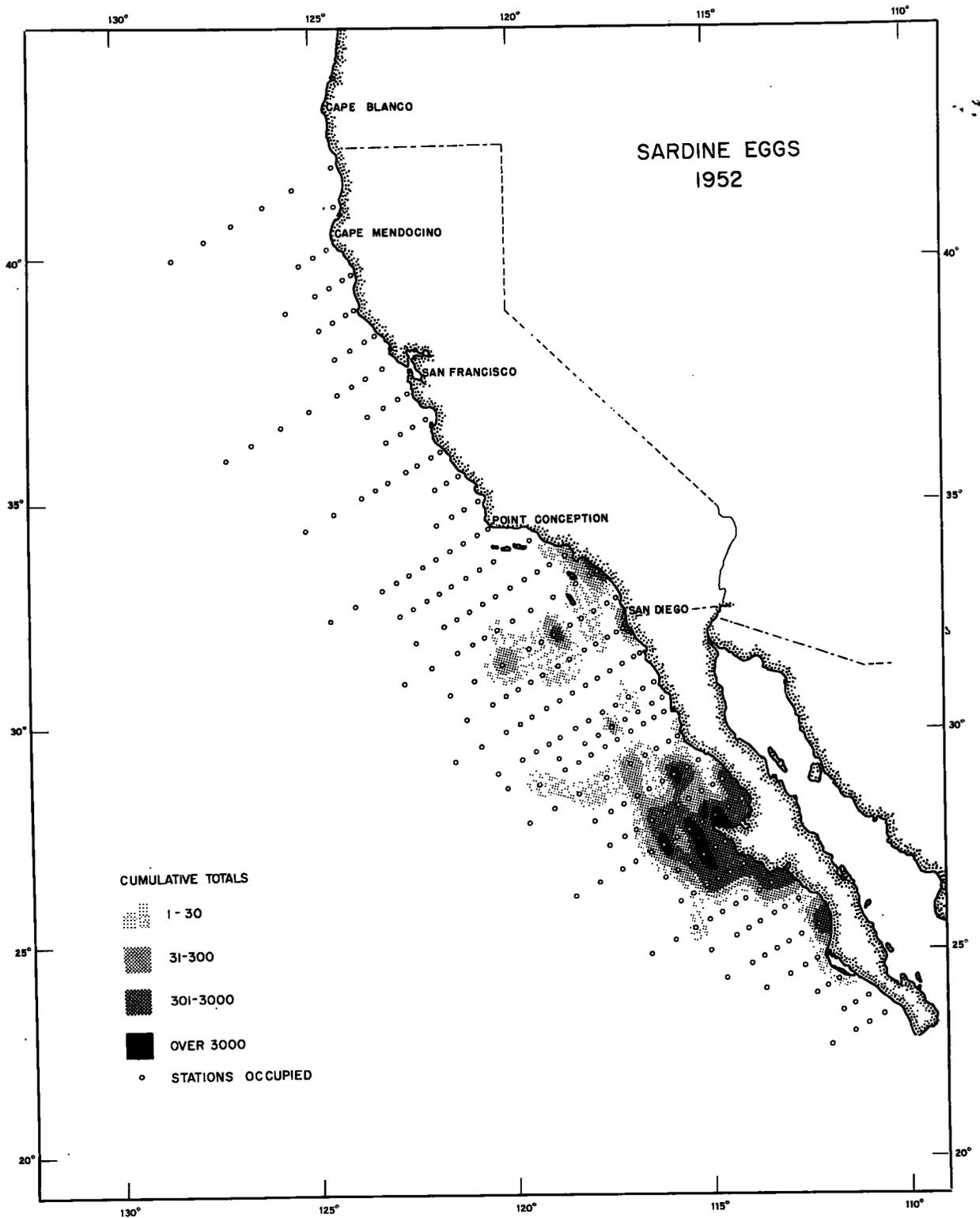


FIGURE 3.—Distribution and abundance of sardine eggs in 1952.

TABLE 2.—Estimated number of sardine eggs in survey areas, 1952

[In billions; cruise number in parentheses]

Area	January (5201)	February (5202)	March (5203)	Late March (5203)	April (5204)	May (5205)	June (5206)	July (5207)	August (5208)	September (5209)	October (5210)	November (5211)	Total	Percent
North of Point Concep- tion:														
Lines 40-57					0	0	0	0	0	0	0	0	0	0
60-77					0	0	0	0	0	0	0	0	0	0
Total					0	0	0	0	0	0	0	0	0	0
Southern California:														
Line 80	0	0	0		0	0	0	0	0	0	0	0	0	0
83					0	0	0	10	0	0	0	0	10	0
87					118	0	0						118	0
90	3	0	80		0	613	16	412	8	0	0	0	1,132	0
93	0	0	59		378	908	58	0	0	0	0	0	1,403	0
Total	3	0	139		496	1,521	74	422	8	0	0	0	2,663	1.96
Northern Baja California:														
Line 97	0	0	471		18	26	67	0	0	0	0	0	582	0
100	0	0	0		0	0	4	0	0	0	0	0	4	0
103					14	0	0	0	0	0	0	0	14	0
105	0	0	1,030										1,030	0
107					0	0	0	0	0	0	0	0	0	0
Total	0	0	1,501		32	26	71	0	0	0	0	0	1,630	1.20
Upper central Baja California:														
Line 110	20	0	322		0	0	341	0	0	0	0	0	683	0
113		0	16,736	0	3,398	4,251	1,420	74	0	0	0	0	25,879	0
115	0												0	0
117		631	6,765	0	1,135	3,743	2,427	122	119	1,871	0	12	16,825	0
120	972	5,280	222	405	10,239	7,422	4,675	1,860	5,512	5,294	0	0	41,881	0
Total	992	5,911	24,045	405	14,772	15,416	8,863	2,056	5,431	7,165	0	12	85,268	62.67
Lower central Baja California:														
Line 123	602	203	383	3,249	6,802	2,682	111	66	0	3,024	38	8	17,168	0
127	0	0	1,802	4,399	962	554	153	0	0	0	498	0	8,368	0
130	848	13	0	156	41	0	0	0	8,819	0	0	0	9,877	0
133	0	20	14	0	0	26	0	0	0	0	0	0	60	0
137	0	902	0	0	0	0	10,029	0	0	0	0	0	10,931	0
Total	1,450	1,138	2,199	7,804	7,805	3,262	10,293	66	8,819	3,024	536	8	46,404	34.11
Southern Baja California:														
Line 140		19											19	0
143		64											64	0
147		0											0	0
150		0											0	0
Total		83											83	.06
Grand total	2,445	7,132	27,884	8,209	23,105	20,225	19,301	2,544	14,458	10,189	536	20	136,048	100.00
Percent	1.8	5.2	20.5	6.0	17.0	14.9	14.2	1.9	10.6	7.5	0.4	0	100.0	

of spawning within these centers during the period covered by this report.

There was very little sardine spawning to the north of the central Baja California area in 1952—only 3.2 percent of the total. Sardine spawning in the southern spawning area centered off Point San Eugenio. Less spawning, proportionately, occurred to the south of Point San Eugenio than in 1950 or 1951.

The largest portion of sardine eggs are usually spawned by the 2- and 3-year-old fish, since these ages usually make up the dominant portion of the spawning population. The 1949 and 1950 year classes were the weakest on record, based on numbers landed by the commercial fishery. Each

year class supplied only about 130 million fish to the commercial catch. For comparison, it may be noted that the 1939 class supplied 7,500 million fish; the 1947 class, 3,100 million; and the 1948 class, 2,100 million. Undoubtedly, the low egg estimate for 1952 reflects the low numbers of 3-year-old fish of the 1949 class and 2-year-old fish of the 1950 class in the spawning stock.

DISTRIBUTION AND ABUNDANCE OF SARDINE EGGS IN 1953

The estimated abundance of sardine eggs by station lines in 1953 is given in table 3, and the distribution is illustrated in figure 4. Cruises

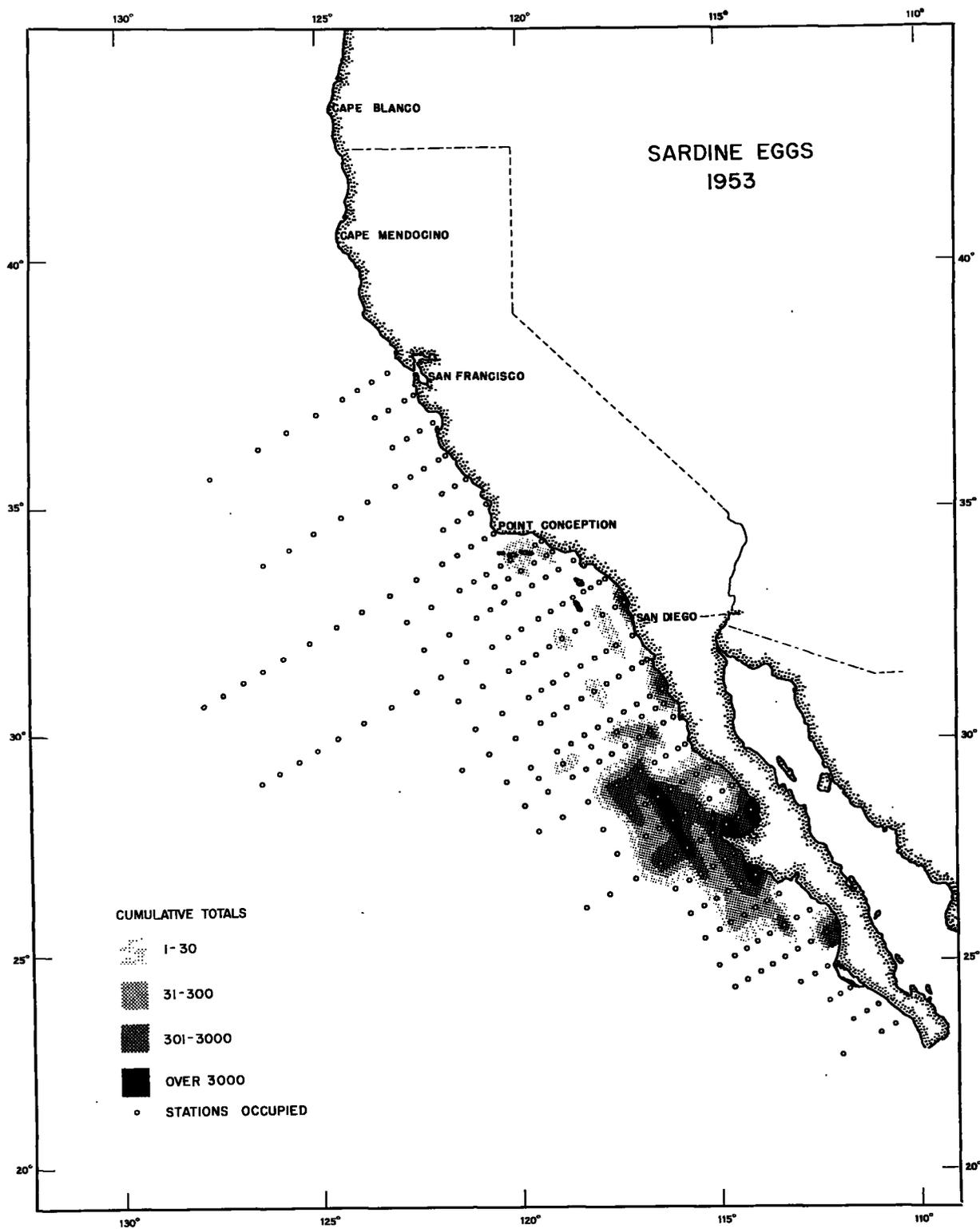


FIGURE 4.—Distribution and abundance of sardine eggs in 1953.

TABLE 3.—Estimated number of sardine eggs in survey areas, 1953

[In billions; cruise number in parentheses]

Area	January (5301)	February (5302)	March (5303)	Late March (5303)	April (5304)	May (5305)	June (5306)	July (5307)	August (5308)	September (5309)	October (5310)	November (5311)	December (5312)	Total	Percent
North of Point Conception: Lines 60-77					0	0	0	0	0					0	
Total					0	0	0	0	0					0	
Southern California:															
Line 80	0	0	0		0	0	0	0	0					0	
83	0	20	0		0	7	12	0	0	0	0	0	0	39	
85	0	0	0		2	0	0	0	0	0	0	0	0	2	
87	0	0	0		0	0	0	0	0	0	0	0	0	0	
90	0	0	0		0	0	0	0	0	0	0	0	0	0	
93	0	0	0		0	29	12	593	0		0	0	0	634	
Total	0	20	0		2	36	24	593	0	0	0	0	0	675	0.15
Northern Baja California:															
Line 97	0	0	0		0	0	18	0	0		0		0	18	
100	0	2	0		0	7	0	0	0		0		0	9	
103					0	981	33	0	0		0		0	1,014	
105	0	671	294											965	
107					1,199	0	0	0	0		0		0	1,199	
Total	0	673	294		1,199	988	51	0	0		0		0	3,205	0.73
Upper central Baja California:															
Line 110	0	0	823		2,298	1,515	0	0	0		0		0	4,636	
113	0	131	9,079	608	1,394	29	2,026	0	0	0	0		432	13,699	
115										0				0	
117	0	21,759	2,480	0	1,083	4,607	1,222	0	77	3,532	0		0	34,760	
120	136	15,497	35	286	10,260	4,022	310	29,047	148,907	4,196	124		1,250	214,070	
Total	136	37,387	12,417	894	15,035	10,173	3,558	29,047	148,984	7,728	124		1,682	267,165	60.70
Lower central Baja California:															
Line 122	0	0	55	568	154	125	0	6,956	382		874		0	9,114	
127	0	2,600	0	23	67	594	13	145,225	213		476		0	149,211	
130	0	406	108	25	0	171	0	0	0		0		0	710	
132	0	0	0	0	0	0	35	0	1,633		0		0	1,668	
137	0	0	0	0	0	0	92	7,871	455		0		0	8,418	
Total	0	3,006	163	616	221	890	140	160,052	2,683		1,350		0	169,121	38.42
Southern Baja California:															
Line 140	0													0	
143	0													0	
147	0													0	
150	0													0	
Total	0													0	0
Grand total	136	41,086	12,874	1,510	16,457	12,087	3,773	189,692	151,667	7,728	1,474	0	1,682	440,166	
Percent	<0.1	9.3	2.9	0.3	3.7	2.8	0.9	43.1	34.5	1.8	0.3	0	0.4	100.0	100.00

were made during all months of 1953, although the cruises in September and November covered only a part of the usual survey area.

The distribution of eggs in 1953 was similar to the distribution in 1952, as can be seen by a comparison of figures 3 and 4. Very little spawning occurred to the north of the central Baja California area—less than 1 percent of the total. Water temperatures were lower during the spring months of 1953 than in any recent season, especially in the inshore waters off southern California and northern Baja California. These data are presented in a later section of this report.

During the first half of 1953, most of the spawning occurred in the upper central Baja California area, offshore from Sebastian Viscaïno Bay (sta-

tion lines 110-120). The heaviest spawning of the year, however, occurred in July and August, centered within Sebastian Viscaïno Bay and along shore in the area between Point San Eugenio and Point San Juanico. This late-season spawning was the heaviest of any recent year.

DISTRIBUTION AND ABUNDANCE OF SARDINE EGGS IN 1954

The distribution of sardine eggs in 1954 is shown in figure 5; their estimated abundance in table 4. Ten cruises were made in 1954, representing every month except September and November. As can be seen from the spacing of stations in figure 5, a more intensive survey of spawning areas was made in 1954 than in previous years.

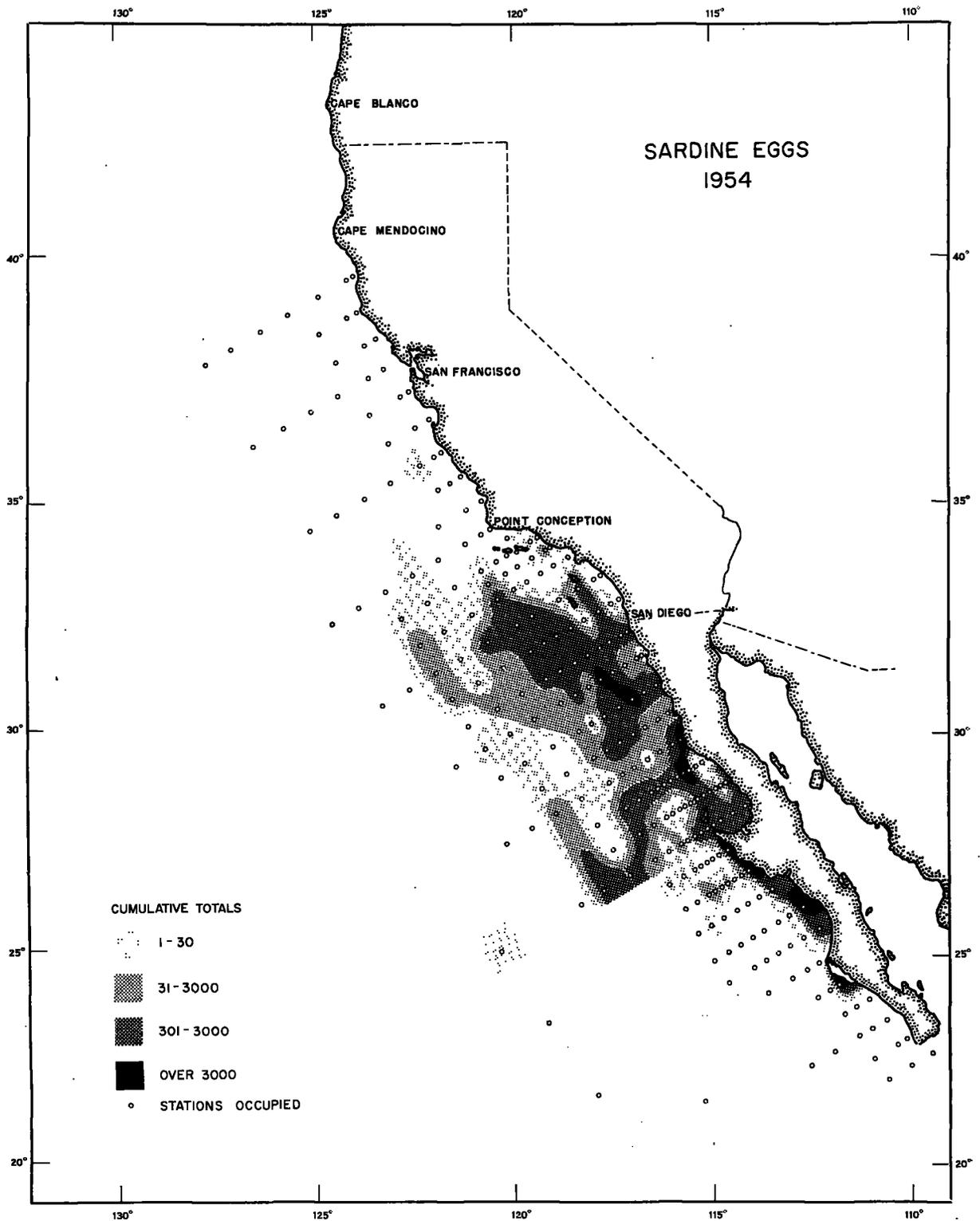


FIGURE 5.—Distribution and abundance of sardine eggs in 1954.

TABLE 4.—Estimated number of sardine eggs in survey areas, 1954

[In billions; cruise number in parentheses]

Area	January (5401)	February (5402)	March (5403)	April (5404)	May (5405)	June (5406)	July (5407)	August (5408)	October (5410)	December (5412)	Total	Percent
North of Point Conception: Lines 60-77.....	0	0	0	0	0	38	0	0	0	-----	38	0.01
Total.....	0	0	0	0	0	38	0	0	0	-----	38	0.01
Southern California:												
Line 80.....	0	0	0	0	0	67	0	0	0	0	67	
83.....	0	17	0	0	99	132	7	0	0	0	255	
85.....	0	2	2	3	0	75	385	0	0	0	467	
87.....	0	0	0	208	4,559	197	19	0	0	0	5,043	
90.....	0	0	0	1,801	1,093	6,662	11,317	0	0	0	20,873	
93.....	0	0	0	3,214	6,661	10,576	0	0	0	0	20,451	
Total.....	0	19	2	5,286	12,412	17,709	11,728	0	0	0	47,156	13.27
Northern Baja California:												
Line 97.....	0	0	4,174	7,254	1,561	13,215	128	170	0	0	26,502	
100.....	2	0	2,725	972	16,538	4,217	139	0	0	0	24,598	
103.....	39	10	4,096	15,951	3,251	1,672	5,714	0	0	0	30,733	
107.....	0	40	604	2,798	278	4,045	37	0	0	0	7,802	
Total.....	41	50	11,599	26,975	21,628	23,149	6,018	170	0	0	89,630	25.22
Upper central Baja California:												
Line 110.....	26	110	1,207	3,950	5,371	334	0	0	0	0	10,998	
113.....	0	6,022	10,037	8,128	3,860	2,940	0	0	0	0	30,996	
117.....	26	461	3,883	941	4,365	101	241	0	0	0	10,018	
120.....	21,595	6,660	8,752	298	94	338	8,016	7,252	0	232	53,207	
Total.....	21,647	13,253	23,879	13,287	13,890	3,722	8,257	7,252	0	232	105,219	29.61
Lower central Baja California:												
Line 123.....	3,431	27,879	3,593	88	0	0	643	13	0	200	35,847	
127.....	380	9,235	4,652	407	108	22	324	0	0	0	15,128	
130.....	0	28	0	0	0	12	2,285	0	0	0	2,325	
133.....	0	48	0	0	0	0	40,297	0	0	0	40,345	
137.....	44	0	0	0	2,142	1,418	0	0	0	141	3,745	
Total.....	3,855	37,190	8,245	495	2,250	1,452	43,549	13	0	341	97,390	27.41
Southern Baja California:												
Line 140.....	0									0	0	
143.....	15,925									0	15,925	
147.....	0									0	0	
150.....	0									0	0	
Total.....	15,925									0	15,925	4.48
Grand total.....	41,468	50,512	43,725	46,043	49,980	46,070	69,552	7,435	0	573	355,358	100.00
Percent.....	11.7	14.2	12.3	13.0	14.1	13.0	19.6	2.1	0	0.2	100.2	

The most striking feature of sardine spawning in 1954 was its northward spread to waters off southern California and northern Baja California. It is by far the greatest contrast that has been observed between successive seasons. In 1953, sardine eggs were obtained in only 20 hauls in the northern center (station lines 80-107), while in 1954 they were taken in 149 hauls. In 1953, the distribution was discontinuous; in only two instances were sardine eggs taken in contiguous hauls. In 1954, the distribution was continuous over widespread areas. Only 4×10^{12} eggs are estimated to have been spawned in the northern center in 1953, while 137×10^{12} are estimated to have been spawned in 1954. Interpreting these figures literally, there were approximately 35 times as many spawning fish in the northern center in 1954 as in 1953.

The estimate of egg abundance for the area off central Baja California of 203×10^{12} eggs constitutes approximately 57 percent of the total number taken during 1954. The late-season spawning was much less important in 1954 than in 1953; less than 30 percent of the estimated total number of eggs in the central Baja California region was obtained during the last half of the year.

DISTRIBUTION AND ABUNDANCE OF SARDINE EGGS IN 1955

The estimated abundance of sardine eggs in 1955 is summarized by month and station line in table 5. Relative abundance in different parts of the spawning area is illustrated in figure 6. The August cruise of 1955, the wide-ranging Norpac expedition, is not included in the tabulations. No sardine eggs and only 27 sardine larvae were obtained on Norpac.

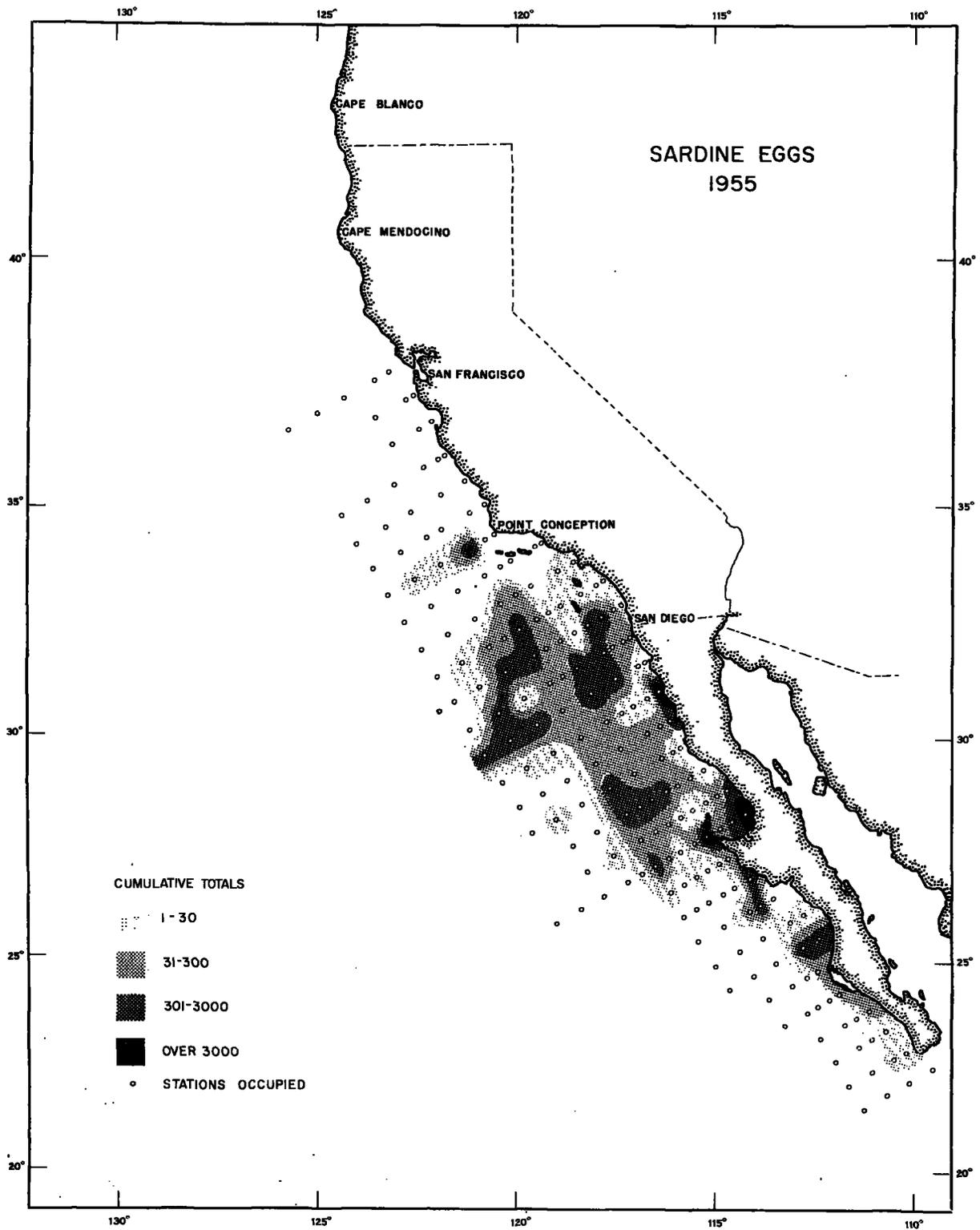


FIGURE 6.—Distribution and abundance of sardine eggs in 1955.

TABLE 5.—Estimated number of sardine eggs in survey areas, 1955

[In billions; cruise number in parentheses]

Area	January (5501)	February (5502)	March (5503)	April (5504)	May (5505)	June (5506)	July (5507)	August (5508) ¹	Septem- ber (5509)	October (5510)	Novem- ber (5511)	Decem- ber (5512)	Total	Per- cent
North of Point Concep- tion: Lines 60-77.....					0	0	0			0			0	
Total.....					0	0	0			0			0	0
Southern California:														
Line 80.....	0	0	0	0	0	4,379	0			0		0	4,379	
83.....	0	0	0	0	0	0	0		0	0	0	0	0	
87.....	0	0	0	0	0	309	56		0	0	0	0	365	
90.....	0	0	250	278	1,031	277	40		0	0	0	0	1,876	
93.....	0	0	1,511	64	6,153	3,714	0		0	0	0	0	11,442	
Total.....	0	0	1,761	342	7,184	8,679	96		0	0	0	0	18,062	11.11
Northern Baja Cali- fornia:														
Line 97.....	0	0	1,342	11,288	10,101	572	0			0		0	23,303	
100.....	0	0	4,687	23,690	2,152	33	0			0		0	30,562	
103.....	0	6,268	60	1,277	147	48	36			0		8	7,844	
107.....	9	3,117	579	2,188	34	17	0			0		0	5,944	
Total.....	9	9,385	6,668	38,443	12,434	670	36			0		8	67,653	41.90
Upper central Baja California:														
Line 110.....	0	2,838	165	263	7	0	0			0		0	3,273	
113.....	12,238	4,910	4,424	675	0	0	0			0		0	22,247	
117.....	18	119	526	622	1,122	299	259			240		0	3,205	
120.....	5,280	871	1,382	9	6,693	6,505	4,234			1,972		377	27,323	
Total.....	17,536	8,738	6,497	1,569	7,822	6,804	4,493			2,212		377	56,048	34.46
Lower central Baja California:														
Line 123.....	47	0	32	0	0	0	17			0		433	529	
127.....	0	0	0	0	0	0	0			0		1,834	1,834	
130.....	0	0	0	0	0	0	6,028			0		0	6,028	
133.....	0	0	0	0	0	21	0			62		0	83	
137.....	2,697	0	0	0	8,230	0	0			0		0	10,927	
Total.....	2,744	0	32	0	8,230	21	6,045			62		2,267	19,401	11.93
Southern Baja Califor- nia:														
Line 140.....	0	0	0									0	0	
143.....	0	434	0									0	434	
147.....	939	0	0									0	939	
150.....	58	0	0									0	58	
153.....	47	0	0									0	47	
157.....	0	0	0									0	0	
Total.....	1,044	434	0									0	1,478	0.91
Grand total.....	21,333	18,557	14,958	40,354	35,670	16,174	10,670		0	2,274	0	2,652	162,642	100.01
Percent.....	13.1	11.4	9.2	24.8	21.9	9.9	6.6		0	1.4	0	1.6	99.9	

¹ Norpac.

The distribution of eggs in 1955 was almost as widespread as in 1954. More than 50 percent of the eggs were obtained in the northern center, with the heaviest spawning occurring on lines 93-100, between Del Mar, Calif., and Ensenada, Baja California.

There were only 18 occurrences of sardine eggs to the south of Point San Eugenio during 1955 (lower central Baja California area). This represented a marked decrease from preceding seasons. Only about 13 percent of the spawning occurred in this area in 1955 as compared with 52 percent in 1951, 34 percent in 1952, 38 percent in 1953, and 27 percent in 1954.

The late-season spawning (July to December) was not adequately sampled in 1955. The only

regular cruises made off central Baja California after July were in October and December. Because of this, the 1955 estimate is too low by perhaps 10 or 15 percent.

DISTRIBUTION AND ABUNDANCE OF SARDINE EGGS IN 1956

The survey area in 1956 was covered fairly completely during January through July, but only partially thereafter. The area between Point Conception, Calif., and Point San Juanico, Baja California (lines 80-137), was covered on monthly cruises between January and July 1956; the area to the north of Point Conception (lines 60-77) was covered in April through June; the area off southern Baja California in January, February,

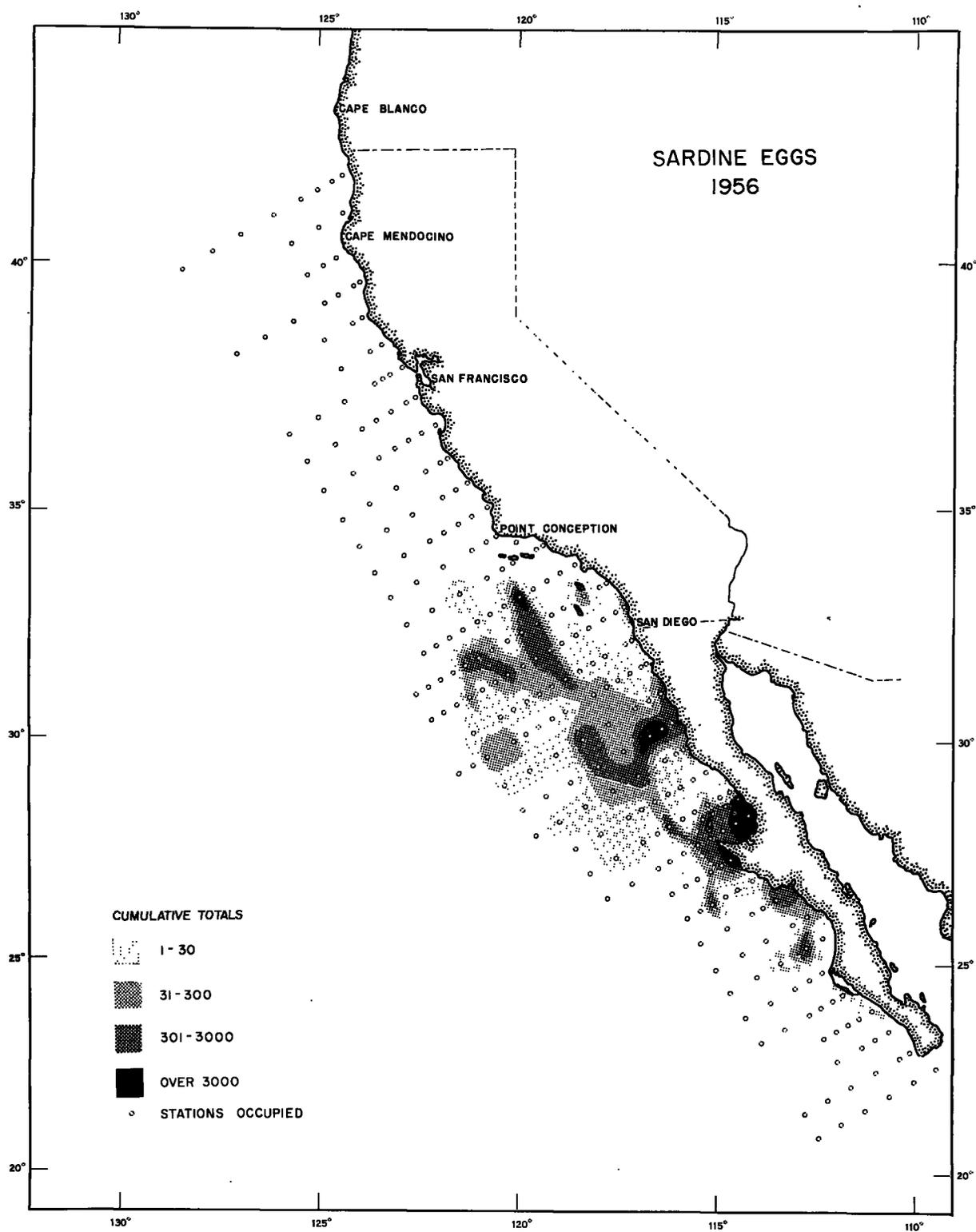


FIGURE 7.—Distribution and abundance of sardine eggs in 1956.

and April. After July, the cruises covered only a portion of the usual survey area: in August and September the portion off central Baja California; in October through December the portion off southern California and one station line off northern Baja California (lines 80-97).

The distribution of sardine eggs in 1956 (fig. 7) was similar to that in 1954, although areas of high concentration of eggs were less widespread. The heaviest spawning in 1956 was in the Sebastian Viscaïno Bay region in July (table 6). The percentage of spawning that occurred in the northern center was lower than in the preceding year: 37.3 percent in 1956, as compared with 52.7 percent in 1955. Spawning in the northern spawning

center, however, had a wider distribution than in the southern center (table 7).

The 1956 season was unusual in several respects. There was less difference in temperatures in different parts of the spawning range than in any recent year (table 12); furthermore, the temperatures throughout the spawning range were the lowest of any year between 1951 and 1956.

AREAL DISTRIBUTION OF SPAWNING

The marked change in the distribution of sardine spawning that occurred between the 1953 and 1954 seasons has been briefly commented on in the discussion of the distribution and abundance of sardine eggs in 1954. This difference will be

TABLE 6.—Estimated number of sardine eggs in survey areas, 1956

[In billions; cruise number in parentheses]

Area	January (5601)	February (5602)	March (5603)	April (5604)	May (5605)	June (5606)	July (5607)	August (5608)	September (5609)	October (5610)	November (5611)	December (5612)	Total	Per- cent
North of Point Conception: Lines 60-77				0	0	0							0	0
Total				0	0	0							0	0
Southern California:										0	0	0	0	
Line 80	0	0	0	0	0	0	0			0	0	0	0	
83	0	0	0	16	0	8,631	0			0	0	0	16	
87	0	0	0	0	44	8,631	10			0	0	0	8,685	
90	0	0	39	0	12,123	480	364			0	0	0	13,006	
93	0	0	38	0	6,379	1,043	0			83	0	0	7,543	
Total	0	0	77	16	18,546	10,154	374			83	0	0	29,250	11.43
Northern Baja California:														
Line 97	0	0	261	48	2,378	120	9			0	0	0	2,816	
100	0	0	93	2,490	442	0	0						3,025	
103	0	27	2,125	3,032	96	17,241	700						23,221	
107	0	0	4,707	136	44	26,456	5,923						37,266	
Total	0	27	7,186	5,706	2,960	43,817	6,632			0	0	0	66,328	25.91
Upper central Baja California:														
Line 110	0	10	1,669	2,216	9	0	0	0	0				3,904	
113	0	90	286	85	0	0	0	0	0				461	
115													0	
117	4	5,806	0	17	580	0	29	13,102	0				19,338	
120	2,588	576	6,560	17	9,732	186	64,133	9,418	6,520				99,730	
Total	2,592	6,282	8,515	2,335	10,321	186	64,162	22,520	6,520				123,433	48.22
Lower central Baja California:														
Line 123	0	5,910	2,054	366	0	0	0	0	0				8,330	
127	0	39	0	16,013	0	0	0	0	0				16,052	
130	0	1,230	0	0	0	0	0	0	0				1,230	
133	0	0	0	0	0	0	0	1,063	0				1,063	
137	0	0	0	0	0	10,156	0	0	0				10,156	
Total	0	7,179	2,054	16,379	0	10,156	0	1,063	0				36,831	14.39
Southern Baja California:														
Line 140	0	0		0									0	
143	82	0		0									82	
147	0	75		0									75	
150	0	0		0									0	
153	0	0		0									0	
157	0	0		0									0	
Total	82	75		0									157	0.06
Grand total	2,674	13,563	17,832	24,436	31,827	64,313	71,168	23,583	6,520	83	0	0	255,999	100.01
Percent	1.0	5.3	7.0	9.6	12.4	25.1	27.8	9.2	2.6	<0.1	0	0	100.0	

further developed by considering the areal distribution of spawning in the northern and southern spawning centers during 1952 through 1956.

The areal extent of spawning has been estimated for each spawning center by cruise. The results are summarized in table 7. Yearly summaries based on the summation of areal distributions of monthly cruises follow:

Year	Northern center (lines 80-107)	Southern center (lines 110-137)	Total
	<i>Square miles</i>	<i>Square miles</i>	<i>Square miles</i>
1952.....	27,824	89,920	117,744
1953.....	14,560	90,224	104,784
1954.....	149,904	137,680	287,584
1955.....	120,912	76,208	197,120
1956.....	80,368	55,120	135,488

The areal extent of sardine spawning in 1954 was 2.7 times as great as in 1953. Compared with the distribution in 1952 it was 2.4 times as great, 1.5 times as great as in 1955, and 2.1 times as great as in 1956. There was not only a tenfold increase in the extent of spawning in the northern center

(lines 80-107) in 1954 as compared with 1953, but there was an increase in the area over which spawning extended in the southern center (lines 110-137), as well.

Not only was sardine spawning spread over a greater area in 1954 than in any other year in the series, there was also a greater extent of moderately heavy to very heavy concentrations of eggs (101 or more eggs per standard area per day) than in other years (refer to table 8). This point is illustrated in figure 8. The moderately heavy to very heavy categories of table 8 are grouped together in this figure as heavy, while the light and moderate categories of table 8 are designated as light. In 1954, the extent of heavy spawning was greater in both the northern and southern spawning areas than in the other years.

There are two possible explanations for the marked increase in spawning in the northern center in 1954: either the sardines moved into the area from another area or areas, or the sardines had been in the northern center all of the time, but few of them had spawned in 1952 and 1953.

TABLE 7.—Estimated area over which sardine spawning took place summarized by cruise for the northern and southern centers, 1952-56

[In square miles]

	Northern center (lines 80-107)					Southern center (lines 110-137)				
	1952	1953	1954	1955	1956	1952	1953	1954	1955	1956
January.....	256	0	752	720	0	5,840	960	28,656	13,440	1,696
February.....	0	1,600	1,728	7,936	1,200	10,960	11,360	24,976	10,496	12,976
March.....	7,712	4,800	26,784	26,080	28,096	11,248	16,672	25,792	14,800	15,616
April.....	8,336	1,840	44,640	39,856	15,824	15,824	14,000	20,144	14,100	7,968
May.....	5,680	3,120	33,400	22,416	20,800	14,144	14,592	14,128	5,088	3,296
June.....	3,520	2,880	36,302	21,360	11,312	13,104	10,464	12,160	3,792	6,128
July.....	1,820	320	5,700	1,568	2,816	4,704	4,688	6,800	5,648	2,256
August.....	800	0	448	Norpac	-----	7,390	8,880	2,928	Norpac	3,984
September.....	0	0	-----	0	-----	4,560	3,712	-----	-----	1,200
October.....	0	0	0	0	320	1,200	1,872	0	5,152	-----
November.....	0	0	0	0	0	976	-----	-----	-----	-----
December.....	0	0	0	576	0	-----	3,024	2,096	3,632	-----
Total.....	27,824	14,560	149,904	120,912	80,368	89,920	90,224	137,680	76,208	55,120

TABLE 8.—Relative areal distribution of sardine spawning, grouped according to intensity of spawning in the northern and southern centers, 1952-56

[In square miles]

Abundance	Number of eggs per standard area per day	Northern center (lines 80-107)					Southern center (lines 110-137)				
		1952	1953	1954	1955	1956	1952	1953	1954	1955	1956
Light.....	1-10.....	19,984	9,040	72,728	58,480	42,960	30,624	30,752	67,816	39,808	28,784
Moderate.....	11-100.....	7,584	3,920	44,312	41,296	22,222	33,584	29,712	33,088	17,280	11,024
Moderate heavy.....	101-1,000.....	256	1,600	31,264	20,560	13,168	23,712	23,856	32,456	18,128	11,808
Heavy.....	1,001-10,000.....	0	0	1,600	576	2,018	2,000	4,080	4,320	992	3,504
Very heavy.....	Over 10,000.....	0	0	0	0	0	0	1,824	0	0	0
Total.....	-----	27,824	14,560	149,904	120,912	80,368	89,920	90,224	137,680	76,208	55,120

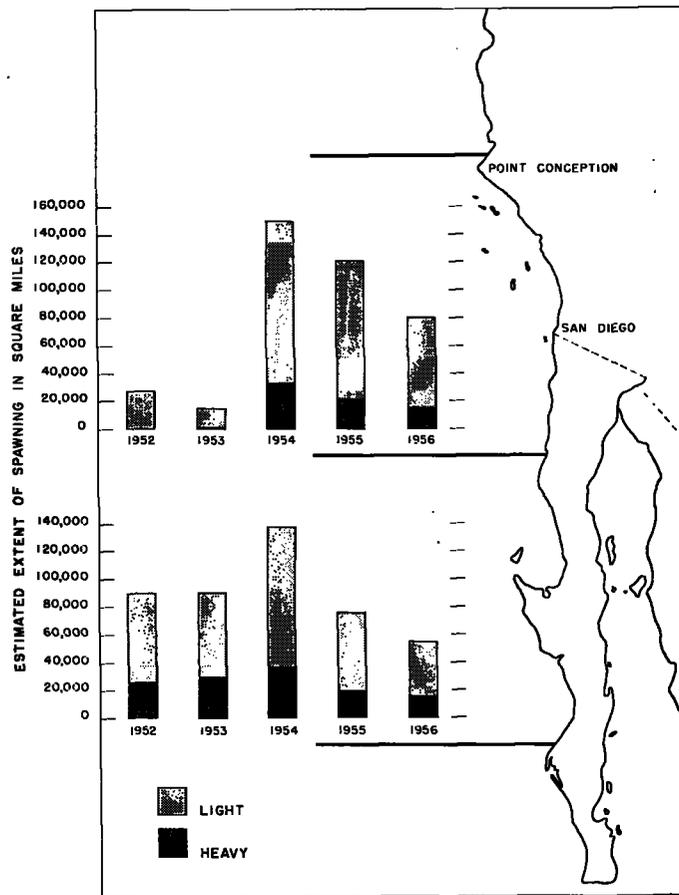


FIGURE 8.—Estimated relative areal extent of spawning in the northern (lines 80-107) and southern centers (lines 110-137).

The second alternative is not supported by evidence from the fish catch. The commercial catch of sardines pointed to a very low abundance in the northern center in 1952 and 1953. The commercial catch (in California) in 1952-53 amounted to only 4,520 tons, in 1953-54 to 3,172 tons, while it jumped to 67,258 tons in 1954-55.

Emigration into the area is the only explanation that satisfactorily accounts for both the increase in eggs spawned in the northern center in 1954 and the marked increase in fish available to the fishery in the 1954-55 season. The only likely areas that sardines could have migrated from are those to the south. There seems to be little doubt, therefore, that sardines moved into the northern spawning center from the southern center off central Baja California.

There is no categorical answer to the question, "Why did the spreading out of spawning occur?" At least two explanations should be given careful

consideration: (1) The movement was a result of change in environmental conditions, and (2) the movement was the result of population pressure.

If the change in distribution resulted from a change in the physical environment that favored emigration, the most likely change would involve water temperatures, directly, or as an indicator of other qualities of significance to spawning sardines.

In order to study temperature changes within the northern spawning center, the area was divided into four quadrants. The northeast section (inshore, southern California) was identical to the area surveyed in 1940 and 1941; the northwest portion consisted of all stations occupied on lines 80-93 to the seaward of the inshore section. The southeast portion consisted of all stations on lines 97 to 107 between shore and station 50 inclusive; the offshore quadrant comprised all stations occupied to the seaward of station 50 on lines 97-107.

Average temperatures at a depth of 10 meters for the winter and spring seasons of 1951 through 1956 are given in table 9 for the four quadrants of the northern spawning center. There was nothing unusual about winter and spring temperatures in 1954. For the northern center as a whole, the winter temperatures were less than 0.1° C. higher than the 6-year average; the spring temperatures were 0.25° C. higher than the average. In the sections contiguous to the southern spawning center, the southeast and southwest areas that emigrating sardines would first enter, the temperatures were somewhat above average in the inshore quadrant (0.17° C. in January–March and 0.50° C. in April–June) and somewhat below average in the offshore quadrant in the winter period (0.25° C. lower than average) and close to average in the spring period. There was only 0.02° C. difference between the average winter temperatures in the northern spawning center in 1952 as compared with 1954—two markedly contrasting years with regard to distribution and abundance of spawning in the northern center. Temperatures in 1953, the year with the least spawning in the northern center, were not much below average in the winter period (0.11° C.), but were the coldest in the series during the spring months (0.61° C. below the 6-year average).

TABLE 9.—Average water temperatures at a depth of 10 meters in northern spawning center based on all stations occupied

[Lines 80-107]

Date	Temperature (° C.) in—				
	Northeast section	Northwest section	Southeast section	Southwest section	Northern center
January–March:					
1951.....	13.34	14.92	14.72	15.87	14.71
1952.....	13.59	13.86	14.41	15.08	14.24
1953.....	13.33	13.98	14.24	14.71	14.06
1954.....	13.90	13.93	14.46	14.73	14.26
1955.....	13.46	13.67	14.26	14.72	14.03
1956.....	12.79	13.78	13.65	14.67	13.72
Average.....	13.40	14.02	14.29	14.96	14.17
April–June:					
1951.....	14.34	14.51	15.46	16.14	15.11
1952.....	14.09	14.75	14.23	16.16	14.81
1953.....	12.90	14.29	14.16	15.57	14.23
1954.....	14.20	14.75	15.52	15.90	15.09
1955.....	14.28	14.21	15.63	15.70	14.96
1956.....	14.22	14.30	15.10	15.76	14.84
Average.....	14.00	14.47	15.02	15.87	14.84

Temperature data for the years 1952 through 1956 will be published in *Oceanic Observations of the Pacific*, of which only one volume in the series, observations for 1949, has appeared as yet (Rakestraw, Horrér, and Wooster, 1957).

In a subsequent section, there is a discussion of temperatures at which sardine eggs were obtained during the years 1951 through 1956. I do not wish to anticipate results before presenting the data, but the difference was more marked between temperatures at which sardine eggs were obtained in the two major spawning centers in 1952 and 1953 than in the other years.

An alternative explanation for the emigration is that population pressure had increased to such an extent in the southern center that a portion of the population moved out. Some data can be marshaled in support of this thesis, some against it. Two lines of evidence will be considered: virtual population estimates and estimates of the number of eggs spawned.

It is possible to derive minimal estimates of the size of the spawning population each year from virtual population (accumulated age) estimates. These estimates are based on age composition data from the commercial catch (Felin, Anas, Daugherty, and Pinkas, 1952; Felin, MacGregor, Daugherty, and Miller, 1953, 1954, and 1955; Felin, Wolf, Daugherty, and Miller, 1958; Wolf, MacGregor, Daugherty, and Miller, 1958). Each estimate represents those sardines of 2 years of age and older that were definitely present in the population in a given season, since they were subsequently caught. Availability influences virtual population estimates, since only those fish can be caught that are present in the fishing area. Also, differences in fishing intensity and natural mortality of sardines are not taken into account. Hence, the estimates are minimal.

Virtual population estimates for seasons 1951 through 1955 are compared with estimates of sardine egg abundance in the following tabulation. Recent estimates of the virtual population are low, because some year classes used in the estimates have made only a partial contribution to the fishery as yet. The 1956 estimate of the virtual population is not included for this reason.

Year	Virtual population estimate (in billions) ¹	Estimate of sardine egg abundance
1951.....	1.20	610×10 ¹²
1952.....	.38	136×10 ¹²
1953.....	.67	436×10 ¹²
1954.....	1.17	355×10 ¹²
1955.....	0.75	163×10 ¹²

¹ Minimal size of spawning population.

There is fair correspondence between the virtual population estimates and the estimates of sardine egg abundance for every season except 1953. In this season the estimate of egg abundance is too large in comparison with the virtual population estimate. As noted previously, most of the sardine eggs obtained in 1953 resulted from fall spawning in the southern center, and it is unlikely that the group of late-season spawners ever became fully available to the California fishery. Only about 89×10^{12} eggs were taken during the main spawning period in 1953 (table 12).

The virtual spawning population in 1954 was the largest for any season since 1951. The increase could have resulted in moderate population pressure. However, the amount of spawning off central Baja California in 1954 was only 35 percent as much as in 1951, when spawning remained concentrated in the southern spawning center.

The widespread spawning in 1954 is interesting for another reason. In a consideration of factors that might favorably influence the survival of a year class, I have theorized (Ahlstrom 1950, p. 45) that the extent of the area over which spawning was spread was probably one of the more important ones: the larger the area, the greater the chance of a good survival. The 1954 distribution gave us an opportunity to test this hypothesis. The areal extent of sardine spawning in 1954 was greater than in any other recent year. The 1954 class had poor survival during the larval stage and has, to date, contributed very little to the fishery (larval survival for 1952-56 classes will be presented in a later publication). It appears to be nearly as weak as the very poor 1949 and 1950 classes, and has contributed only 85 million fish to the catch as 1- to 3-year-old fish. If this judgment is born out by its subsequent history in the fishery, then we must question the importance of wide areal distribution in the production of a successful year class.

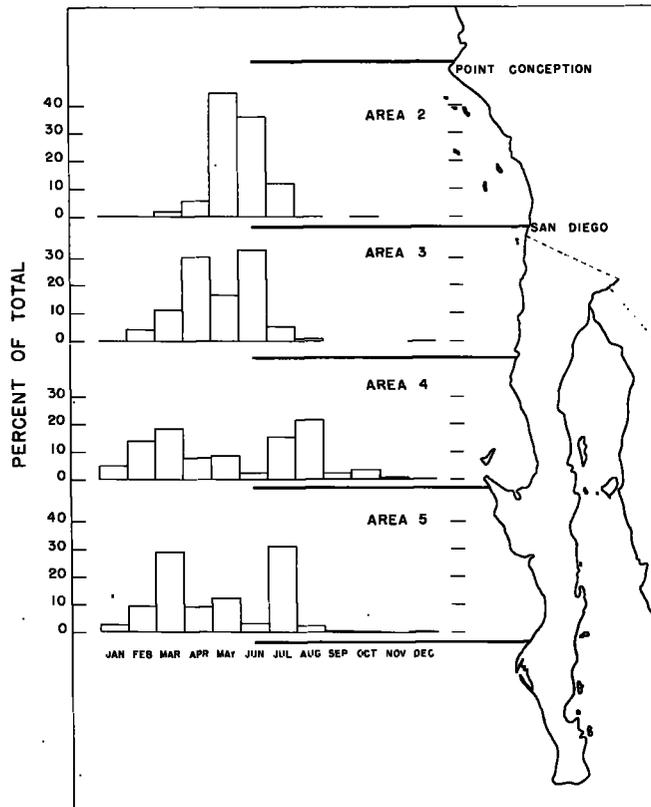


FIGURE 9.—Average seasonal distribution of sardine spawning, 1951-56, by area. (Area 1 omitted; see footnote to table 10.)

The relation between sardine spawning in the northern center and availability of sardines to the commercial fishery during the subsequent fishing season has been briefly mentioned for 1952 through 1954. The relation during the 5-year period, 1952 through 1956, is given in the following tabulation:

Spawning season	Estimated abundance of eggs in northern spawning center	Percentage of total spawning	Commercial fishing season (Oct. 1-Feb. 1)	California commercial catch (tons)
1952.....	4×10^{12}	3.2	1952-53	4,520
1953.....	4×10^{12}	.9	1953-54	3,170
1954.....	137×10^{12}	38.5	1954-55	67,260
1955.....	86×10^{12}	52.7	1955-56	74,980
1956.....	96×10^{12}	37.3	1956-57	32,650

Sardine spawning was negligible in the northern center in 1952 and 1953, and the commercial catch was exceedingly poor. With the return of a sizable spawning population to the northern spawning center in 1954, the commercial catch immediately jumped to 67,260 tons. It could have been larger during this season, as a price dispute delayed the opening of the San Pedro season for about 5 weeks. The 1955-56 catch was the best during the 5-year period. The catch during the 1956-57 season started out well. Sardines were moving southward during the brief period of good fishing and were not available in any numbers to the southern California fishery during the remainder of the season.

SEASONAL DISTRIBUTION OF SPAWNING 1951-56

The monthly occurrences and abundance of sardine eggs in different parts of the spawning range are summarized in table 10 for the 6-year period, 1951-56. Average seasonal distributions are illustrated in figure 9. The 1950 season is not included because the coverage of spawning areas was less intensive and complete than in succeeding years.

Southern California area (lines 80-93)

Approximately 98 percent of the eggs spawned in this area have been obtained during the 4-month period, April through July. The month of peak spawning has been either May (1951, 1952, 1956), June (1954, 1955), or July (1953). Based on totals for six seasons (1951-56), nearly 45 per-

cent of the sardine eggs were obtained in May, 35 percent in June. There have been only three occurrences of sardine eggs in the months of August through January. Some spawning has taken place during February and March, but it usually has been light; about 10 percent of the occurrences off southern California were recorded for these months, but only about 2 percent of the number of eggs spawned.

Northern Baja California area (lines 97-107)

The areas off southern California and northern Baja California together constitute the northern spawning center. As off southern California, there have been only negligible amounts of spawning during August through January (six occurrences, 0.11 percent of eggs spawned). Spawning has occurred somewhat earlier in the year off northern Baja California, however. More than 45 percent of the sardine eggs were obtained during February through April in this area, whereas less than 8 percent were obtained during these months off southern California. Since 1954, there have been considerably more occurrences of eggs in this area than off southern California. Based on totals for the six seasons, approximately 30 percent of sardine eggs were obtained in April and 33 percent in June.

Upper central Baja California area (lines 110-120)

Sardine eggs have been collected throughout the year in this area. The composite seasonal distribution, based on the totals for 6 years, is bimodal, with peaks in March and August. Spawning during the first half of the year usually has a much wider areal distribution than spawning during the latter half. As is shown later, spawning during the main spawning period has taken place at temperatures that were only slightly higher than those encountered in the northern spawning center, but that were fully 2.5° C. lower than the average temperature of spawning of the late-season group.

Late-season spawning usually is confined to the southern end of Sebastian Viscaïno Bay in the upper central Baja California area (lines 110-120) and to inshore stations along the coast in the lower central Baja California area (lines 123-137). As is pointed out later, late-season spawners may constitute a separate subpopulation of

TABLE 10.—Occurrences and abundance of sardine eggs, by area and month, 1951-56

Area and month	Occurrence of eggs							Estimated number of eggs (in billions)								
	1951	1952	1953	1954	1955	1956	Total	1951	1952	1953	1954	1955	1956	Total	Percent	
Southern California (lines 80-93):																
January	0	1	0	0	0	0	1	0	3	0	0	0	0	0	3	<0.01
February	1	0	2	2	0	0	5	0	0	20	19	0	0	39	.03	
March	2	3	0	1	3	3	12	211	139	0	2	1,761	77	2,190	1.93	
April	6	4	1	13	5	1	30	302	406	2	5,286	342	16	6,344	5.99	
May	4	7	3	18	14	14	60	10,927	1,521	36	12,412	7,184	18,546	50,626	44.99	
June	6	2	3	18	15	8	52	4,065	74	24	17,709	8,679	10,154	40,705	35.89	
July	3	2	1	5	2	2	15	315	422	593	11,728	96	374	13,528	11.96	
August	0	1	0	0	(?)	0	1	0	0	0	0	0	0	0	0	
September	0	0	0	0	0	0	0	0	0	0	0	0	83	83	.07	
October	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	
November	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
December	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Total	22	20	10	57	39	29	177	15,720	2,663	675	47,156	18,062	29,250	113,526	100.00	
Northern Baja California (lines 97-107):																
January	0	0	0	2	1	0	3	0	0	0	41	9	0	50	.02	
February	0	0	2	2	7	19	12	0	0	673	50	9,385	27	10,135	4.10	
March	3	3	2	19	12	19	58	61	1,501	294	11,599	6,668	7,186	27,309	11.05	
April	6	2	2	28	24	11	73	2,676	32	1,199	26,975	38,443	5,706	75,030	30.36	
May	8	1	2	17	14	11	53	2,355	26	988	21,628	12,434	2,960	40,391	16.34	
June	7	2	2	16	9	7	43	13,546	71	51	23,149	670	43,817	81,304	32.90	
July	0	0	0	6	1	3	10	0	0	0	6,018	36	6,632	12,686	5.13	
August	1	0	0	1	(?)	0	2	42	0	0	170	0	0	212	0.09	
September	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
October	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
November	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
December	0	0	0	0	1	0	1	0	0	0	0	8	0	8	<.01	
Total	25	8	10	91	60	52	255	18,679	1,630	3,205	89,630	67,653	66,328	247,125	99.99	
Upper central Baja California (lines 110-120):																
January	2	4	1	10	7	2	26	1,026	992	136	21,647	17,536	2,592	43,929	4.92	
February	3	5	7	20	10	9	54	52,336	5,911	37,387	13,253	8,738	6,282	123,907	13.87	
March	8	10	17	25	9	13	82	87,204	24,450	13,311	23,879	6,497	8,515	163,856	18.34	
April	10	11	14	26	14	4	79	22,894	14,772	15,035	13,257	1,569	2,335	69,802	7.81	
May	9	14	10	25	5	5	68	19,491	15,416	10,173	13,690	7,822	10,321	76,913	8.61	
June	3	13	10	18	4	4	52	393	8,863	3,558	3,722	6,804	186	23,526	2.63	
July	2	5	2	4	4	3	20	26,396	2,056	29,047	8,257	4,493	64,162	134,411	15.04	
August	3	7	4	3	(?)	6	23	6,916	5,631	148,984	7,252	0	22,520	191,303	21.41	
September	1	4	11	4	0	2	18	308	7,165	7,726	0	0	6,520	21,719	2.43	
October	3	0	1	0	5	0	9	30,736	0	124	0	2,212	0	33,072	3.70	
November	2	1	0	0	0	0	3	6,932	12	0	0	0	0	6,944	.78	
December	3	0	4	1	2	0	10	1,933	0	1,682	232	377	0	4,224	.47	
Total	49	74	81	132	60	48	444	256,473	85,268	267,165	105,219	56,048	123,433	893,606	100.01	
Lower central Baja California (lines 123-137):																
January	3	3	0	3	2	0	11	10,410	1,450	0	3,855	2,744	0	18,459	2.68	
February	2	4	4	4	0	4	18	17,262	1,138	3,006	37,190	0	7,179	65,775	9.55	
March	5	13	9	4	1	3	35	177,801	10,003	779	8,245	32	2,054	198,914	28.87	
April	4	9	3	5	0	3	24	39,687	7,805	221	4,495	0	16,379	64,587	9.37	
May	3	4	8	2	2	0	19	68,162	3,262	890	2,250	8,230	0	82,794	12.02	
June	0	4	3	3	1	2	13	0	10,293	140	1,452	21	10,156	22,062	3.20	
July	1	1	3	4	3	0	12	3,814	66	160,052	43,549	6,045	0	213,526	30.99	
August	2	2	7	1	(?)	1	13	2,705	8,819	2,653	13	0	1,063	15,283	2.22	
September	1	2	0	0	0	0	3	47	3,024	0	0	0	0	3,071	.45	
October	0	2	2	0	1	0	5	0	536	1,360	0	62	0	1,948	.28	
November	0	1	0	0	0	0	1	0	8	0	0	0	0	8	<.01	
December	1	0	0	2	3	0	6	38	0	0	341	2,267	0	2,646	.38	
Total	22	45	39	28	13	13	160	319,926	46,404	169,121	97,390	19,401	36,831	699,073	100.01	
Southern Baja California (lines 140-157):																
January			0	1	4	1	6			0	15,925	1,044	82	17,051	96.37	
February		2			1	1	4		83			434	75	562	3.35	
March	0				0		0	0				0		0	0	
April							0	0						0	0	
May														0	0	
June	2						2	50						50	.28	
July																
August					(?)											
September	0						0	0						0	0	
October																
November														0	0	
December				0			0				0			0	0	
Total	2	2	0	1	5	2	12	50	83	0	15,925	1,478	157	17,663	100.00	

¹ Area 1 omitted. Only two collections containing sardine eggs were obtained in area 1 (to the north of Point Conception): One in June 1951, the other in June 1954.

² Norpac.

sardines. Although the separation of regular spawning from the late-season spawning is much sharper in some seasons than others, I am considering eggs spawned between January and June in this area to belong to the regular spawning group, and eggs spawned during July through December to result from another spawning group.

Lower central Baja California area (lines 123-137)

The composite seasonal distribution of sardine spawning in the lower central Baja California area is bimodal with peaks in March and July. In the 6-year period, 1951-56, about two-thirds of the spawning in this area occurred during the main spawning period, and one-third during the late spawning period. Sampling has been less intensive during the latter half of the year, consequently abundance of eggs during these months has been somewhat underestimated.

The lower central Baja California area decreased in importance as a spawning center between 1950 and 1956. In 1950 and 1951, approximately 50 percent of the total sardine spawning occurred in this area, while in 1955 and 1956 less than 15 percent of sardine eggs were taken here.

Southern Baja California area (lines 140-157)

During the 6-year period under consideration, only 13 cruises extended into the area off southern Baja California. Nine cruises were made in January through March, and the remaining four were made during April, June, September, and December. Sardine eggs were taken in 12 hauls. 6 made during January, 4 during February, and 2 during June. Collections in which eggs were common were obtained only in January.

WATER TEMPERATURE AT TIME OF SPAWNING

There have been no direct observations on sardine spawning, consequently water temperatures at time of spawning have been inferred from temperature observations taken at stations where sardine eggs were obtained.

Studies on vertical distribution of sardine eggs have shown that the eggs are limited in their distribution to the upper mixed layer and the upper portion of the thermocline (Silliman 1943; Ahlstrom 1959). The depth of the upper mixed layer varies from station to station and also at a

given station on different occupancies. Sardine eggs have been found to be variously distributed within the mixed layer. In some situations they have been concentrated near the surface or within the upper 10 to 20 meters of depth, at other places they have had a fairly wide distribution within the upper mixed layer or they have been distributed only in the lower portion of the layer.

Although no one level can be representative of the depth distribution of sardine eggs under all conditions, yet on the average the largest concentrations of eggs have been obtained between the surface and about 20 meters. The temperature at a depth of 10 meters has been used in the following analysis. The temperature at this level is much less influenced by diurnal changes than the surface temperature. It is much simpler to obtain than an average temperature for the upper mixed layer, although in many situations it would be identical with such an average and seldom would differ from it by as much as 0.5° C.

In the following analysis, the spawning season has been divided into two parts: main spawning period, extending from January through July in the northern center, January through June in the southern center, and late-season spawning, occurring during July through December in the southern center. Temperature observations are available for 913 collections of sardine eggs made during the major spawning period in 1951 through 1956, and for 121 collections made during the late spawning period.

The frequency of occurrence of sardine eggs at different temperatures is given in table 11 and illustrated in figure 10. Observations from the several geographical areas are summarized separately. Temperature observations are grouped by 0.5° C. intervals.

The temperature range over which sardine eggs were obtained during the major spawning period was from 11.0° to 21.2° C. Approximately 93 percent of the occurrences were at temperatures between 13.0° and 17.9° C., and more than 50 percent of the occurrences were within a 1½° C. range (14.5-15.99° C.). The mean, median, and modal temperatures for the spawning range as a whole fall in the same interval, 15.0-15.49° C. The majority of occurrences at temperatures below 13° C. were in the adjacent 0.5° interval. So few sardine eggs have been taken at temperatures be-

TABLE 11.—Relation between water temperature and occurrence of sardine eggs, 1951-56

Temperature at 10 meters (° C.)	Occurrences of sardine eggs during—								
	Main spawning period on lines—						Late-season spawning on lines—		
	80-83	97-107	110-120	123-137	140-157	Total	110-120	123-137	Total
11.0-11.49	1	2				3	1		1
11.5-11.99	2	2				4			4
12.0-12.49	5	2	3	2		12			12
12.5-12.99	6	6	5	4		21	1		1
13.0-13.49	13	8	5	3		29			29
13.5-13.99	22	12	8	5		47	2		2
14.0-14.49	37	31	27	10		105		3	3
14.5-14.99	34	53	58	15		160			160
15.0-15.49	17	56	79	17		169	2	2	4
15.5-15.99	6	31	84	20		141	2	3	5
16.0-16.49	10	25	55	8		98	5	4	9
16.5-16.99	8	15	20	8	1	52	5	1	6
17.0-17.49	4	6	12	5	2	29	10	3	13
17.5-17.99	4		2	12	1	19	7	6	13
18.0-18.49	2			3	2	7	6	1	7
18.5-18.99		2		1	1	4	11	4	15
19.0-19.49	1			3		4	8		8
19.5-19.99				1	3	4	12	1	13
20.0-20.49	1	1			1	3	4	2	6
20.5-20.99					1	1	2	2	4
21.0-21.49		1				1	2	1	3
21.5-21.99							1	1	2
22.0-22.49								1	1
23.0-23.49								1	1
23.5-23.99								3	3
27.0-27.49								1	1
Total	173	253	358	117	12	913	81	40	121
Average	14.7	15.1	15.4	15.7	18.7	15.2	18.1	18.0	18.1

low 13° C. that this temperature can be considered a threshold for Pacific sardine spawning.

During the late spawning period (July-December), sardine eggs were obtained at temperatures between 11.3° and 27.4° C. The average temperature for the 6-year period was 18.1° C. Thus, late-season spawning occurred, on the average, at temperatures which were 2.9° C. higher than during the major spawning period. Less than 3 percent of the occurrences during the major spawning period were at temperatures above 18.0° C., while more than 50 percent of the occurrences during the late spawning period were at temperatures of 18° C. or above.

This marked difference between the average temperature at spawning of the major spawning group of sardines and of the late-season spawning fish has raised the question of whether the late-season spawners may not constitute a separate subpopulation. The subpopulation problem in the Pacific sardine is discussed by Marr (1957). Although the question has been posed from a consideration of time and temperature differences at spawning, the problem will have to be solved by other techniques such as genetic studies of spawning fish of the two groups, growth studies, and a suitable tagging program.

If the late-season spawners off central Baja

California do not constitute a separate subpopulation, then one of two explanations must apply: either spawning throughout the year off central Baja California is carried on by the same group of fish, or the late-season spawning is carried on principally by young fish spawning for the first time, probably as 1½-year-old fish. The latter explanation is an appealing one, for if true, it would mean that the late-season spawning could be used to assess the strength of each year class when approximately 1½ years of age.

It is important to know whether the late-season spawners do constitute a separate subpopulation or not. If they are a separate subpopulation with different environmental requirements than the main group of sardines, they may be largely unavailable to the California commercial fishery. Because of this possibility, estimates of egg abundance from late-season spawners have been separated from those of the main spawning group in table 12.

The fluctuation in abundance of eggs is considerably greater during the late-season than during the main spawning period. Sampling during July-December off central Baja California was about equally intensive in 1952 and 1953, yet the estimate of abundance of 352×10^{12} eggs for 1953 was nearly 12 times as large as the estimate of

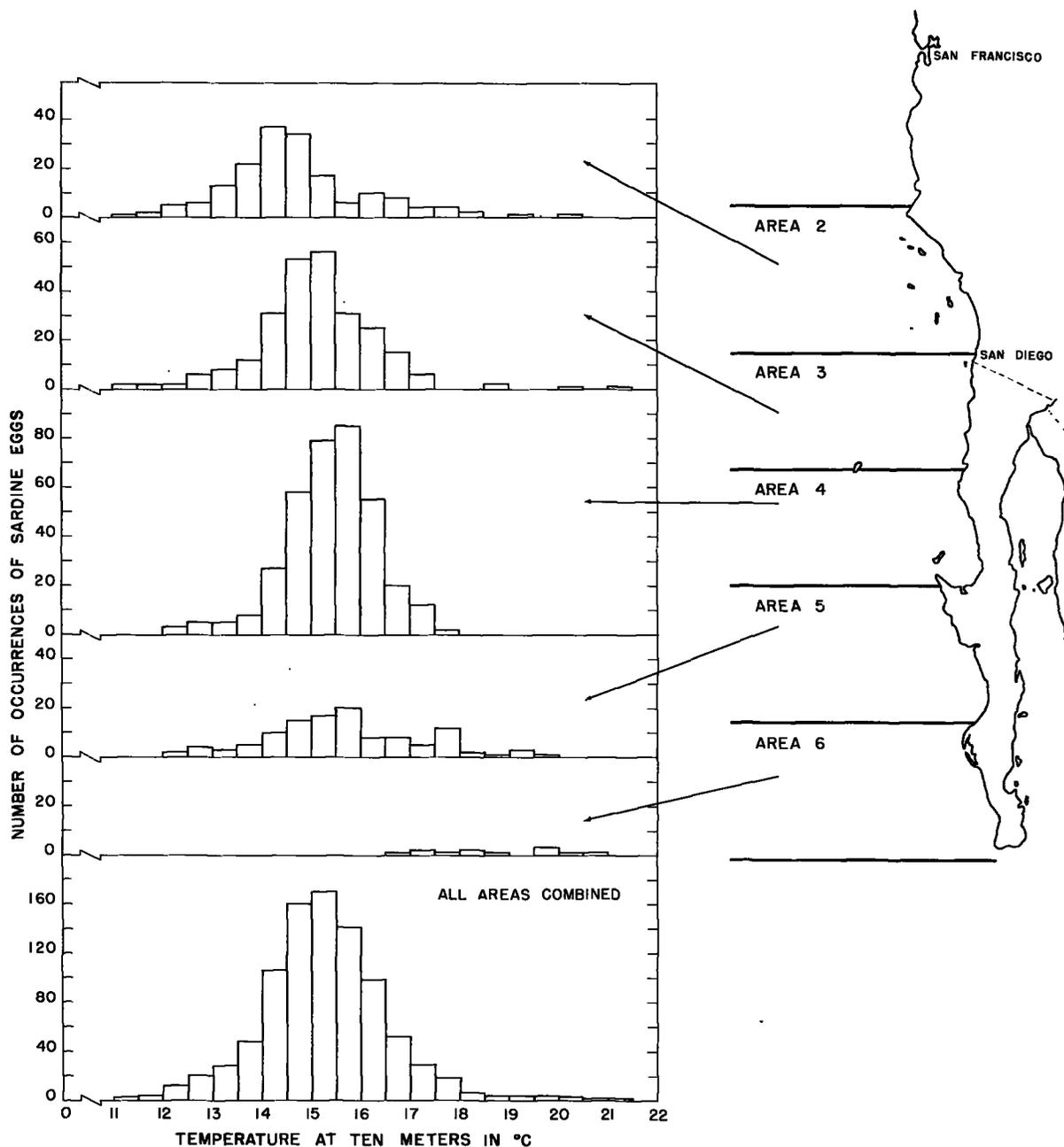


FIGURE 10.—Temperature distribution of sardine eggs during the complete spawning period off southern California and northern Baja California (areas 2 and 3) and during the main spawning period (January-June) off central Baja California (areas 4 and 5) and southern Baja California (area 6).

27×10^{12} eggs for 1952. The lowest estimate of the group, that of 15×10^{12} eggs for 1955, is an underestimate, since collections within the late-season spawning areas were not made during August and September 1955.

Average temperatures at which sardine eggs

were obtained in different parts of the spawning range are summarized for the major spawning period by season and area in table 13. The average temperature increased from north to south. For the 6-year period, 1951-56, the amount of the increase going southward from one area to the

TABLE 12.—Relative contribution to sardine egg estimates of eggs collected during the main spawning period and of eggs collected during late-season spawning, 1951-56

Area	1951		1952		1953		1954		1955		1956	
	Estimated abundance	Percent of total										
Main spawning period:												
North of Point Conception (lines 60-77).....	0	0	0	0	0	0	38	0.01	0	0	0	0
Southern California (lines 80-93).....	15,720	2.57	2,663	1.96	675	0.15	47,156	13.27	18,062	11.11	29,250	11.43
Northern Baja California (lines 97-107).....	18,679	3.06	1,630	1.20	3,205	.73	89,630	25.22	67,653	41.60	66,328	25.91
Upper central Baja California, Jan.-June (lines 110-120).....	183,254	30.00	70,404	51.75	79,600	18.08	89,478	25.18	48,966	30.11	30,231	11.81
Lower central Baja California, Jan.-June (lines 123-137).....	313,322	51.29	33,951	24.96	5,036	1.14	53,487	15.05	11,027	6.78	35,768	13.97
Southern Baja California, Jan.-June (lines 140 & below).....	50	0	83	0.06	0	0	15,925	4.48	1,478	.91	157	.06
Total.....	531,025	86.92	108,731	79.93	88,516	20.10	295,714	83.21	147,186	90.51	161,734	63.18
Late season spawning (July-December):												
Upper central Baja California.....	73,219	11.99	14,864	10.93	187,565	42.61	15,741	4.43	7,082	4.36	93,202	36.41
Lower central Baja California.....	6,566	1.07	12,453	9.15	164,085	37.30	43,903	12.35	8,374	5.15	1,063	.42
Total.....	79,785	13.06	27,317	20.08	351,650	79.91	59,644	16.78	15,456	9.50	94,265	36.83

TABLE 13.—Temperature range and means for stations where sardine eggs were taken, by season and area, for main spawning period

[Temperature (° C.) at 10 m.]

	1951	1952	1953	1954	1955	1956	All years
Southern California (lines 80-93):							
Number of observations.....	22	19	10	55	39	28	173
Temperature range.....	11.8-18.2	12.0-18.2	11.3-16.9	12.8-20.4	12.8-17.9	12.4-17.9	11.3-20.4
Mean temperature.....	14.8	14.5	13.7	14.9	14.7	14.7	14.7
Northern Baja California (lines 97-107):							
Number of observations.....	25	6	10	90	70	52	253
Temperature range.....	11.4-16.9	13.0-15.9	12.6-16.9	11.5-21.2	13.0-17.4	11.2-16.9	11.2-21.2
Mean temperature.....	15.0	14.6	14.8	15.6	15.1	14.5	15.1
Upper central Baja California (lines 110-120):							
Number of observations.....	35	57	59	123	48	36	358
Temperature range.....	12.7-16.5	12.5-17.4	12.7-16.5	12.1-17.9	13.0-16.5	12.2-16.5	12.1-17.9
Mean temperature.....	15.3	15.9	16.1	15.7	15.2	14.6	15.4
Lower central Baja California (lines 123-137):							
Number of observations.....	17	34	27	21	6	12	117
Temperature range.....	13.5-17.9	12.3-19.4	12.8-17.9	12.9-19.9	14.0-15.9	12.4-17.9	12.3-19.9
Mean temperature.....	16.0	15.8	15.3	16.5	15.1	14.7	15.7
Summation (lines 80-137):							
Number of observations.....	99	116	106	289	163	128	901
Temperature range.....	11.4-18.2	12.0-19.4	11.3-17.9	11.5-21.2	12.8-17.9	11.2-17.9	11.2-21.2
Mean temperature.....	15.2	15.6	15.1	15.6	15.0	14.6	15.2
Southern Baja California (lines 140-157):							
Number of observations.....	2	1	1	1	5	2	12
Temperature range.....	17.2-18.1	19.9	20.2	19.7	16.9-20.6	18.2-19.6	16.9-20.6
Mean temperature.....	17.6	19.9	20.2	19.7	18.3	18.9	18.7

next was roughly uniform at approximately 0.3° C. between each of the four principal areas, but jumped to 3.0° C. from lower central Baja California to southern Baja California.

The average temperature at spawning off southern California during the 6-year period was 14.7° C. In only one year, 1953, did the mean temperature depart from this average by more than 0.2° C. The average temperature at spawning off northern Baja California during 1951-56 was 15.1° C.; the range in average temperature values for the individual years was from 14.5° to 15.6° C. The average temperature at spawning in the northern spawning center, which comprises the

above two geographical areas, was 14.9° C. during these years.

Average temperatures at spawning for individual seasons in the upper central Baja California area ranged from 14.6° to 15.9° C.; the average for the 6-year period was 15.4° C. There was a greater spread in the seasonal averages for lower central Baja California, the lowest, 14.7° C. in 1956, being 1.8° C. below the highest, 16.5° C. in 1954. Although there was a 0.3° C. difference between the 6-year average temperatures in the upper and lower central Baja California areas, it should be noted that the average temperatures were almost identical during 4 seasons, and differed by 0.7° to 0.8° C. during the other 2 seasons.

The average temperature at spawning in the southern spawning center (upper and lower central Baja California areas) during the 6-year period was 15.5° C. Thus, the difference in average temperature at spawning in the two major spawning centers was 0.6° C. during the years 1951-56. However, the difference between individual years was as small as 0.1° or 0.2° C. (1955 and 1956) and as large as 1.3° C. (1952), as can be seen from the following summary:

Major spawning period	Average temperature (° C.) in—		Difference (° C.)
	Northern spawnings center (lines 80-107)	Southern spawning center (lines 110-137)	
1951.....	14.9	15.6	+0.7
1952.....	14.5	15.8	+1.3
1953.....	14.2	15.2	+1.0
1954.....	15.3	15.8	+0.5
1955.....	15.0	15.2	+0.2
1956.....	14.5	14.6	+0.1

It is interesting to note that in 1952 and 1953, when there was limited spawning in the northern center, the difference in temperatures between the two centers during the period of spawning was somewhat greater than in the other years.

Although the lowest average temperature in the northern spawning center occurred in 1953, the lowest average temperature throughout the spawning range occurred in 1956 (14.6° C.). The average temperature in the northern center in 1956 was the same as in 1952 and only 0.3° C. higher than in 1953, yet spawning was widespread in the center in 1956 and limited in both amount and extent in 1952 and 1953.

During the years under consideration, the greater abundance of sardine spawning occurred in areas where the average temperature was between 15.0° and 15.9° C. The only exception to this statement is the 1956 season, when average temperatures throughout the spawning range were below 15° C.

Only a limited number of collections of sardine eggs have been obtained off southern Baja California (lines 140-157). In the 6-year period, 1951-56, 12 hauls contained sardine eggs. The temperature range at these stations was from 16.9° to 20.6° C., the mean temperature was 18.7° C. This value is 3° C. higher than the average temperature in the lower central Baja California area during the same period.

Actually, the average temperatures in the southern Baja California area during January through June were as high as the average temperatures during the late-season spawning period, July through December (table 14). If we postulate that the late-season spawning was carried on by a separate subpopulation and use as a major premise the difference in average temperatures between the major spawning period and the late-season spawning, then, by the same reasoning, we are forced to conclude that the sardine spawners off southern Baja California also constitutes a separate subpopulation. I am merely pointing out this fact for consistency, and hasten to add that we have no definite evidence for or against the existence of a separate subpopulation in this area. There is a possibility that the sardines from southern Baja California are more closely allied to sardines in the Gulf of California than to those off central Baja California.

TABLE 14.—Temperature ranges and means for stations where sardine eggs were taken, summarized by years and area, for late-season spawning

[Temperature (° C.) at 10 m.]

Year	Lines 110-120			Lines 123-137		
	Number of observations	Temperature range	Mean temperature	Number of observations	Temperature range	Mean temperature
1951.....	14	17.5-20.9	19.5	5	16.5-23.9	20.4
1952.....	16	11.3-21.4	17.3	8	15.5-23.4	19.1
1953.....	22	15.0-21.9	18.2	12	14.0-23.9	18.9
1954.....	8	16.5-20.4	18.6	7	16.0-20.9	18.1
1955.....	11	13.5-17.9	16.5	7	14.0-16.5	15.3
1956.....	10	16.5-20.4	18.6	1	27.0	27.0
Total.....	81	11.3-21.9	18.1	40	14.0-27.0	18.0

A difficulty in comparing the average temperatures of late-season spawning in different years arises from the paucity of samples in some years. The survey in 1955, for example, was limited to October and December; hence the average temperatures for this year are not strictly comparable with any other year. This is unfortunate, for the limited temperature observations available were markedly lower than during any other season.

RELATION OF EGG ABUNDANCE TO TEMPERATURE

In order to determine whether large concentrations of sardine eggs were taken at temperatures different from those determined for sardine eggs irrespective of abundance, average temperatures

were obtained for those hauls containing 101 or more eggs. The results are summarized by area for the 1951-56 period:

Area	Station lines	All hauls of sardine eggs		Hauls of 101 or more sardine eggs	
		Number of hauls	Average temperature (° C.)	Number of hauls	Average temperature (° C.)
Southern California.....	80-93	173	14.7	51	14.9
Northern Baja California.....	97-107	253	15.1	82	15.2
Upper central Baja California.....	110-120	358	15.4	143	15.3
Lower central Baja California.....	123-137	117	15.7	60	15.6

The average temperature at which hauls containing larger concentrations of sardine eggs were made was very similar to the average for all hauls. In only one instance was the temperature difference between the two groups of hauls as large as 0.2° C.

In an analysis of the relation of jack mackerel larvae to temperature, Ahlstrom and Ball (1954), using temperatures at 20-meter depths, found that hauls containing a large number of larvae (101 larvae or more per haul) were associated with a more limited temperature range, 12.5-17.0° C., and lower mean temperature, 14.75° C., than hauls containing only 1 to 10 larvae. The temperature range for the latter group was from 10.0° to 19.0° C., and the mean temperature was 15.45° C.

TEMPERATURE CONDITIONS IN 1940 AND 1941

Sardine spawning surveys made in 1940 and 1941 covered an area off southern California that presently would be included in the southern California area (Sette and Ahlstrom, 1948; Ahlstrom 1948). The ranges and means of water temperatures at stations where sardine eggs were taken during these years are summarized, by cruise, in table 15. Temperature observations for 1940 were taken from Sverdrup et al. (1944); for 1941 from Sverdrup et al. (1947). The average temperature for the 1940 season was 15.1° C. and for the 1941 season 16.1° C. The average temperature at which sardine eggs were taken in 1940 was 0.2° C. higher than that off southern California during any year between 1951 and 1956, and the average temperature in 1941 was 1.2° C. higher. The average temperature off southern California in

1941 was higher than the average temperature at which sardine eggs were obtained off lower central Baja California (lines 123-137) during 5 of 6 years between 1951 and 1956. We have no information on either sardine spawning or water temperatures off central Baja California in 1941, so cannot compare the temperatures in that region in 1941 with those obtained off southern California.

TABLE 15.—Temperature range and mean for stations where sardine eggs were taken, summarized by cruises, 1940 and 1941

[Temperature (° C.) at 10 m.]

Cruise number	Date	Number of occurrences	Temperature range (° C.)	Mean temperature (° C.)
<i>1940</i>				
10.....	III: 5-14	37	13.65-16.00	15.2
11.....	III: 20-28	31	13.83-15.86	15.0
12.....	IV: 4-14	32	13.28-16.01	14.9
13.....	IV: 22-V: 3	31	12.68-16.62	14.8
14.....	V: 10-21	32	12.56-18.94	15.3
15.....	V: 27-VI: 7	18	13.26-17.32	15.8
Season.....		181	12.59-18.94	15.1
<i>1941</i>				
17.....	III: 21-30	41	14.98-17.86	16.2
19.....	IV: 14-25	35	14.10-16.90	15.4
21.....	V: 8-17	27	14.57-18.79	16.4
23.....	VI: 2-12	18	13.80-18.13	15.7
25.....	VI: 25-VII: 3	11	14.39-19.14	16.5
27.....	VII: 21-28	5	13.47-20.11	18.2
Season.....		137	13.47-20.11	16.1

Temperatures during the 1941 spawning season point up the fact that there can be greater temperature differences between years in a geographical area, such as the southern California area, than are normally encountered in different parts of the spawning range during a spawning season.

SUMMARY

The distribution and abundance of sardine eggs are discussed and illustrated for the years 1952 through 1956.

Distribution of spawning in 1952 and 1953 was mostly confined to the southern spawning center, off central Baja California.

In 1954, a marked change occurred in the distribution of sardine eggs: heavy and widespread spawning occurred off southern California and adjacent northern Baja California (northern spawning center), as well as in the area off central Baja California. There was a ten-fold increase in the extent of sardine spawning in the northern center

in 1954 as compared with 1953, and a 35-fold increase in the abundance of sardine eggs.

The extent of sardine spawning in the northern spawning center was greater than in the southern center in both 1955 and 1956. Compared with 1954, however, there was a progressive decrease in the areal distribution of spawning in these years.

Estimates of numbers of sardine eggs spawned during 1952-56 were as follows: for 1952, 136×10^{12} ; for 1953, 436×10^{12} ; for 1954, 355×10^{12} ; for 1955, 163×10^{12} ; for 1956, 256×10^{12} . The estimate for 1955 is too low by perhaps 15 percent because of lack of sampling in August and September 1955, during the Norpac expedition.

The occurrences of sardine eggs in the northern spawning center were mostly limited to the months of February through July. Off southern California, heavy spawning took place in May and June, while off northern Baja California heavy spawning commenced in April and continued through June.

Sardine eggs were obtained throughout the year in the southern spawning center. To the north of Point San Eugenio (upper central Baja California area), a composite seasonal distribution showed peaks in March and August, while to the south of Point San Eugenio (lower central Baja California) the peaks occurred in March and July.

During the major spawning period, sardine eggs have been collected at temperatures between 11.0° and 21.2° C., with more than half of the observations occurring within a $1\frac{1}{2}^{\circ}$ C. range (14.5° - 15.99° C.). During the late spawning period (July-December), sardine eggs have been collected at temperatures between 11.3° and 27.4° C. The mean temperature of 18.1° C. in the late spawning period was 2.9° C. higher than the mean temperature of 15.2° C. in the major spawning period.

The average temperature at spawning off southern California during the 6-year period was 14.7° C.; off northern Baja California, 15.1° C.; off upper central Baja California, 15.4° C. (major spawning period, January-June); and off lower central Baja California, 15.7° C. (major spawning period, January-June). Thus, the average temperature at which sardine spawning took place increased from north to south in a fairly uniform fashion.

The difference in temperatures between the two principal spawning centers was found to be greater in 1952 and 1953 than in the other years.

A limited number of samples of sardine eggs off southern Baja California were collected at an average temperature that was nearly 3° C. higher than the average temperature in the southern spawning center during the same period of the year.

When sardine eggs were grouped according to abundance, no difference was found in the temperatures at which they occurred.

The average temperature at which sardine eggs were obtained off southern California in 1940 was slightly higher than in any year between 1951 and 1956, but the average temperature in 1941 was more than 1° C. higher.

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RELATION BETWEEN FISH CONDITION
AND POPULATION SIZE IN THE SARDINE
(Sardinops caerulea)

BY JOHN S. MACGREGOR



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ABSTRACT

Data are presented for 15 fishing seasons between 1941 and 1957 showing the year-to-year trends of mean condition factor and mean length of the Pacific sardine (*Sardinops caerulea*) at San Pedro, and the trend of relative population size of the sardine as measured by the California catch. The data for condition factor and length are based on the four major months of the fishing season, October through January.

There is a high degree of inverse correlation between condition factor and catch, and between length and catch, and a high positive correlation between length and condition factor for the 15 seasons. The correlation between condition factor and catch remains high when the condition factor data are analyzed by restricted length groups, but there is no significant within-season correlation between length and condition factor when the data for each of the 15 seasons are analyzed separately. The high inverse correlation between condition factor and population size is interpreted as a cause and effect relation. While population size may also affect length growth, the primary factor causing the high inverse correlation between average length and population size is probably that both length composition and size of the population are affected by the size of the year-class of sardines just entering the population of sardines exploited by the fishery. The positive between-season correlation between condition factor and length is also considered to be a parallel correlation rather than cause and effect.

RELATION BETWEEN FISH CONDITION AND POPULATION SIZE IN THE SARDINE, *SARDINOPS CAERULEA*

By JOHN S. MACGREGOR, *Fishery Research Biologist*, BUREAU OF COMMERCIAL FISHERIES

Stunted growth of some species of fresh-water fishes in densely populated lakes and ponds is a well-known phenomenon to fishery biologists. Hile (1936) reviews in part the less voluminous literature concerning the relation between density of population and rate of growth of marine fishes. I wish to describe the inverse correlation existing between condition factor and population size in a pelagic marine fish, the Pacific sardine (*Sardinops caerulea*), a situation apparently paralleling that of the stunting of fish under conditions of high population density. Stunting reflects growth conditions over a considerable period of time and especially during preadult life. Condition factor reflects recent feeding conditions. Both stunting and low condition factor may be caused by a meager food supply which, in turn, may result from a large population of fish.

This study is a byproduct of fecundity studies (MacGregor 1957) conducted as part of the broader studies of the California Cooperative Oceanic Fisheries Investigations. The California Cooperative Oceanic Fisheries Investigations are carried out under the sponsorship of the California Marine Research Committee by the California Academy of Sciences, the California Department of Fish and Game, the Hopkins Marine Station of Stanford University, the Scripps Institution of Oceanography of the University of California, and the South Pacific Fishery Investigations of the Bureau of Commercial Fisheries of the U.S. Fish and Wildlife Service. The number of eggs spawned by a sardine appears to be more closely related to the weight of the fish than to its length or age. A sardine having a higher condition factor will generally develop a greater number of eggs than one having a lower condition factor, when the two fish are of similar length and age.

However, the increased relative fecundity of a small population having high condition factors does not compensate for the much larger absolute number of eggs that are developed by a large population having lower condition factors and a lower relative fecundity. There is no apparent correlation between year-class size (either absolute or relative to the parent population) and the condition factor of the population that produced that year-class. Relative fecundity as related to condition factor, which in turn is related to population size, may be one component of a complex of factors that tend to retard population fluctuations, preventing unlimited expansion on the one hand and extinction on the other.

I wish to thank the California Department of Fish and Game for the sampling records, the staff of the South Pacific Fishery Investigations, Bureau of Commercial Fisheries, for helpful criticisms and suggestions, and A. H. Vrooman for preparing the illustrations.

METHODS

Condition-factor data were derived from sampling records compiled by the California Department of Fish and Game. In making age and length determinations of the commercial catch of sardines, a number of samples of 50 sardines each were obtained from the commercial catch each season. Among the data obtained for each sample were the standard lengths of the individual fish in millimeters and the total weight of the sample of fish in kilograms. From these were obtained the mean lengths and the mean weights of the 50-fish samples.

Condition factor may be defined as $K = \frac{W \times 10^7}{L^3}$, in which K = condition factor, W = mean weight of fish in grams and L^3 = cube of the mean stand-

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ard length of fish in millimeters. Multiplying W by 10^7 changed K from a 7-place decimal to a more easily handled 3-digit whole number.

Although the condition factor derived from the mean length and mean weight of sardines in a 50-fish sample will differ from the mean of the individual condition factors of the sardines in the sample, the difference is negligible. The fish within any one sample tend to be approximately the same size and have fairly similar condition factors. Condition factors based on the mean weight and mean length of fish in a sample were compared with the mean condition factors based on the average of the 50 condition factors for the individual fish for several samples in which individual fish weights were known. In no case did the K value computed from the mean length and mean weight differ from the mean K value by as much as 1 percent. For example, in one composite 50-fish sample consisting of ten different 5-fish samples taken over a 1-month period, individual condition factors ranged from 118 to 176 with a mean of 138; lengths ranged from 189 mm. to 256 mm. with a mean of 212 mm., and weights ranged from 92 grams to 198 grams with a mean of 132 grams. The condition factor based on mean length and mean weight was 139 or only one K unit higher than the mean condition factor. The condition factors used in this paper are based on samples that are probably all considerably more homogeneous as to length, weight and condition factor than the above composite sample.

The data used are from a period of 15 fishing seasons, 1941-42 through 1956-57 at San Pedro; for each season the observations cover the 4 principal months, October through January. No data are available for December 1953 and for the entire season of 1944-45.

Condition factors are used as a measure of the "fatness," although not necessarily the fat content, of fish. It is assumed that no appreciable change occurs in the specific gravity of the fish. K values may be compared not only among fish of the same length, but also, if it can be shown that there are no changes in body proportions peculiar to any length group within the size range studied, among fish of different lengths.

A second formula often used by fishery workers, and one related to the condition factor formula, is that for weight-length relation. This formula

generally takes the form $W = CL^n$, in which W = weight, C = a constant determined by the data and L^n = length raised to an exponent determined by the data. This formula describes the weight-length relationship of a sample of fish. Hile (1936) discusses the uses of and the differences between the two formulas in considerable detail.

The formula $W = CL^n$ provides for the possibility that changes in body proportions take place at a constantly increasing or decreasing rate throughout the range of data. This is not necessarily true, especially if the range of data includes both immature and adult fish. Theoretically, if n is less than 3, condition factors should decrease with increase in length, and if n is greater than 3, condition factors should increase with increase in length. The value of n can be influenced by sampling irregularities, such as including in the sample fish from different environments or from different years or months when the length ranges of the fish are not comparable in the different sample components. These irregularities, as well as those caused by including immature and adult fish in the same sample, generally show up as high percentages of plus or minus deviations within one or more restricted length ranges within the total length range of the length-weight curve.

Clark (1928) determined the length-weight relation of the Pacific sardine from data based on fish from the commercial catch at San Pedro from January to April 1921, December 1924 to March 1925, November 1925 to March 1926, and December 1926 to May 1927. Also included were a series of fish of less than 150 mm. standard length (70 to 150 mm.; a size range not represented in the commercial catch) taken from January to December 1921. The length range of the fish taken in the commercial fishery samples is fairly well represented throughout each of the months and years during which sampling was conducted. Clark found that the value of n in the formula $W = CL^n$ was 3.15 for this combined sample of fish. She also concluded that sardines smaller than 200 mm. have a different seasonal weight cycle than sardines larger than 200 mm.

In a later paper Clark (1934) further demonstrated that immature sardines have a different seasonal fat cycle than adults. She also stated (1) that the 3.15 value of n was reduced to 3.07 if fish smaller than 150 mm. are omitted; (2) that

there was no significant difference between the length-weight relationships of males and females; (3) that the value of n for San Pedro sardines (longer than 150 mm.) between May and October 1929 was 2.80 and (4) that the value of n for female sardines throughout an entire year, October 1928 to October 1929, was 2.94. These close approximations of n to the cube indicate that condition factors of sardines of different lengths are comparable, at least within certain limits.

A second and more direct method of determining the comparability of condition factors of fish of different lengths is to determine the trend of K when plotted against fish length in a representative sample. Clark (1928) has done this for each of the months January, February, and March. Each monthly sample consisted of fish taken in four different years, but all lengths were represented fairly well in each of the years. Her data indicated an increase in K from a fish length of about 155 mm. to 195 mm., no change in K between 195 mm. and 250 mm. and a slight decrease in K between 250 and 280 mm.

I have used no sardine samples having mean lengths of less than 190 mm., nor samples having mean lengths greater than 240 mm. K values of

sardines within this length range are comparable.

Measures of population size used in this paper are (1) the California commercial catch in tons, (2) the California catch in numbers of fish (3) accumulated age estimates (numbers of fish) Felin and Phillips, 1948; Mosher et al., 1949; Felin et al., 1949, 1950, 1951, 1952, 1953, 1954, 1955 (in press); Wolf et al. (in press); Clark and Marr, 1955. The latter measure is a minimal population estimate based on the Pacific coast commercial catch. Data for additional years have been included with that of Clark and Marr (1955) for accumulated age estimates. The commercial catch is believed to be a good relative measure of population size off the California coast over the 15 seasons covered by the data because the fishery has been intensive over this period. The catch has fluctuated from almost 600,000 tons to about 3,000 tons during this period. The general trend in catch has been downward since the late 1930's with temporary increases in catch following the entries of the relatively large 1946, 1947, 1948, and 1952 year-classes into the fishery. The use of catch data as a relative measure of the size of the sardine population is discussed at some length by Clark and Marr (1955).

TABLE 1.—Basic data for San Pedro commercial sardine fishery, 1941-42 through 1956-57 seasons

Season	Mean condition factor					Mean length					Number of 50-fish samples				
	Oct.	Nov.	Dec.	Jan.	4-month mean †	Oct.	Nov.	Dec.	Jan.	4-month mean †	Oct.	Nov.	Dec.	Jan.	Total
1941-42	126	123	121	117	122	195	197	196	196	196	70	48	38	46	302
1942-43	126	122	119	118	121	203	203	201	199	202	82	77	76	48	283
1943-44	127	125	123	122	124	201	200	202	200	201	84	58	59	47	243
1944-45															
1945-46	131	130	128	126	129	203	203	202	208	204	25	14	13	20	72
1946-47	135	130	130	128	131	201	203	206	210	205	25	16	22	14	77
1947-48	138	135	134	132	135	210	217	221	221	217	20	18	14	9	61
1948-49	134	129	128	128	130	201	200	200	200	200	18	15	15	12	60
1949-50	128	124	123	124	125	200	199	201	205	201	20	11	17	13	61
1950-51	132	131	129	127	130	205	207	213	214	210	35	40	25	30	130
1951-52	129	128	125	129	128	208	211	212	217	212	40	28	20	21	109
1952-53	137	137	135	137	137	232	235	233	232	233	12	15	9	5	41
1953-54	144	140		134	139	215	234		222	224	16	14	0	3	33
1954-55	137	133	127	132	132	205	206	207	209	207	17	28	20	3	68
1955-56	136	133	132	136	134	214	213	215	215	214	33	25	25	11	94
1956-57	140	137	135	134	137	223	226	228	227	226	34	15	5	7	61

† Unweighted average.

CONDITION FACTOR TRENDS

The trends of condition factors of sardines taken at San Pedro from October to January in each of 15 fishing seasons are shown in figure 1. Since the sardine fishermen locate the sardine schools primarily by bioluminescence, the fishery is carried on at night during the dark of the moon. Because of this, the monthly trends are somewhat in error; sardines from portions of two fishing periods are

often included in 1 month, and fishing periods are often divided between 2 months. Comparison of fishing periods would also contain an error since they do not occur at the same time each year.

Nevertheless, the month-to-month trends and the year-to-year changes in condition factors are well marked. It is apparent that condition factors generally decrease as the fishing season progresses, although there is often an increase from December

TABLE 2.—California sardine catch data and estimated population (by accumulated age) for the fishing seasons 1941-42 through 1956-57

Season	California catch ¹		Estimated population ²
	Thousands of tons	Billions of fish	Billions of fish
1941-42	585	5.34	11.5
1942-43	502	3.96	9.1
1943-44	475	3.48	7.0
1944-45	551	3.81	5.8
1945-46	399	2.81	3.6
1946-47	228	1.86	1.7
1947-48	110	0.93	1.4
1948-49	180	1.50	2.7
1949-50	334	2.75	4.3
1950-51	351	2.59	3.7
1951-52	127	0.96	1.2
1952-53	5	.02	0.4
1953-54	3	.02	0.7
1954-55	67	.53	1.2
1955-56	73	.52	0.8
1956-57	33	.19	-----

¹ Felin and Phillips, 1948; Mosher et al., 1949; Felin et al., 1949, 1950, 1951, 1952, 1953, 1954, 1955 (in press); Wolf et al. (in press).

² Clark and Marr, 1955: (1950-51, 1951-52 and 1952-53 seasons corrected and 1953-54, 1954-55 and 1955-56 seasons added on basis of more recent data).

to January. At the beginning of the fishing season (October), the highest condition factor is 144 (1953); the lowest, 126 (1941 and 1942). At the end of the fishing season (January), the highest condition factor is 137 (1953); the lowest 117 (1942).

Over the range of K values observed, the relative measurement, K , equals the absolute measurement, weight in grams, of a 215½ mm. sardine. That is, from $K = \frac{W \times 10^7}{L^3}$ it follows that $L^3 = \frac{W}{K} \times 10^7$, and when $W=K$, $L^3=10^7$, and $L=215\frac{1}{2}$.

TABLE 3.—Correlation between Monterey and San Pedro condition factors

Month	a	b	Number of samples	Observed r	r when $P^1=.05-.02$	r when $P^1=.02-.01$	r when $P^1=.01-.001$
October	-104.32	1.8794	7	.891	-----	-----	.875-.951
November	1.043	1.0435	6	.885	-----	.882-.917	-----
December	5.354	.9798	6	.911	-----	.882-.917	-----
January	25.112	.8062	5	.917	.878-.934	-----	-----

¹ Fisher and Yates, table VI, page 54.

The Monterey data for one point (1948) on the October correlation of figure 3 are not included in figure 2. This is a single 50-fish sample with a mean K of 149 (mean length=196 mm.). That this K value is not aberrantly high is indicated by the K values of the two samples in the 180-189 mm. length group taken at Monterey at the same time. One had a K value of 151 (mean length 186 mm.) and the other, 141 (mean length 185 mm.).

A 215½ mm. sardine is near the midpoint of the range of sardine lengths (190-240) in the samples used.

Some condition factor data are available for sardines landed at Monterey for 8 of the 16 seasons considered. These are compared with San Pedro sardine condition factors for the corresponding months (fig. 2). The number of 50-fish samples is given in parentheses for Monterey condition factors whenever they are based on less than 10 samples. The January, 1947-48, San Pedro sample is based on nine 50-fish samples; all other San Pedro condition factors are based on 10 or more. Not only are the Monterey data meager, but also their relative abundance is greatest during periods when the sardine population was highest and condition factors lowest. It may be seen (fig. 2) that the Monterey condition factor trend generally follows that at San Pedro, but is higher in value at the beginning of the season and about the same toward the end of the season.

The least squares regression of Monterey on San Pedro condition factors for each of the four months are shown in figure 3 and regression statistics and other data in table 3. Although these correlations are based on small samples (numbers of pairs of data), the probabilities (P) that such high correlations would occur by chance alone are relatively low.

Although the K trend appears to drop more sharply from October to January, and although K values are noticeably higher at the beginning of the season in Monterey, the San Pedro K values do bear a relative relation to those of Monterey. Therefore, it is logical to examine the relationship between San Pedro K values (for which the longest series of data are available) with the total California catch (which should be the best measure available of the total sardine population off the coast of California).

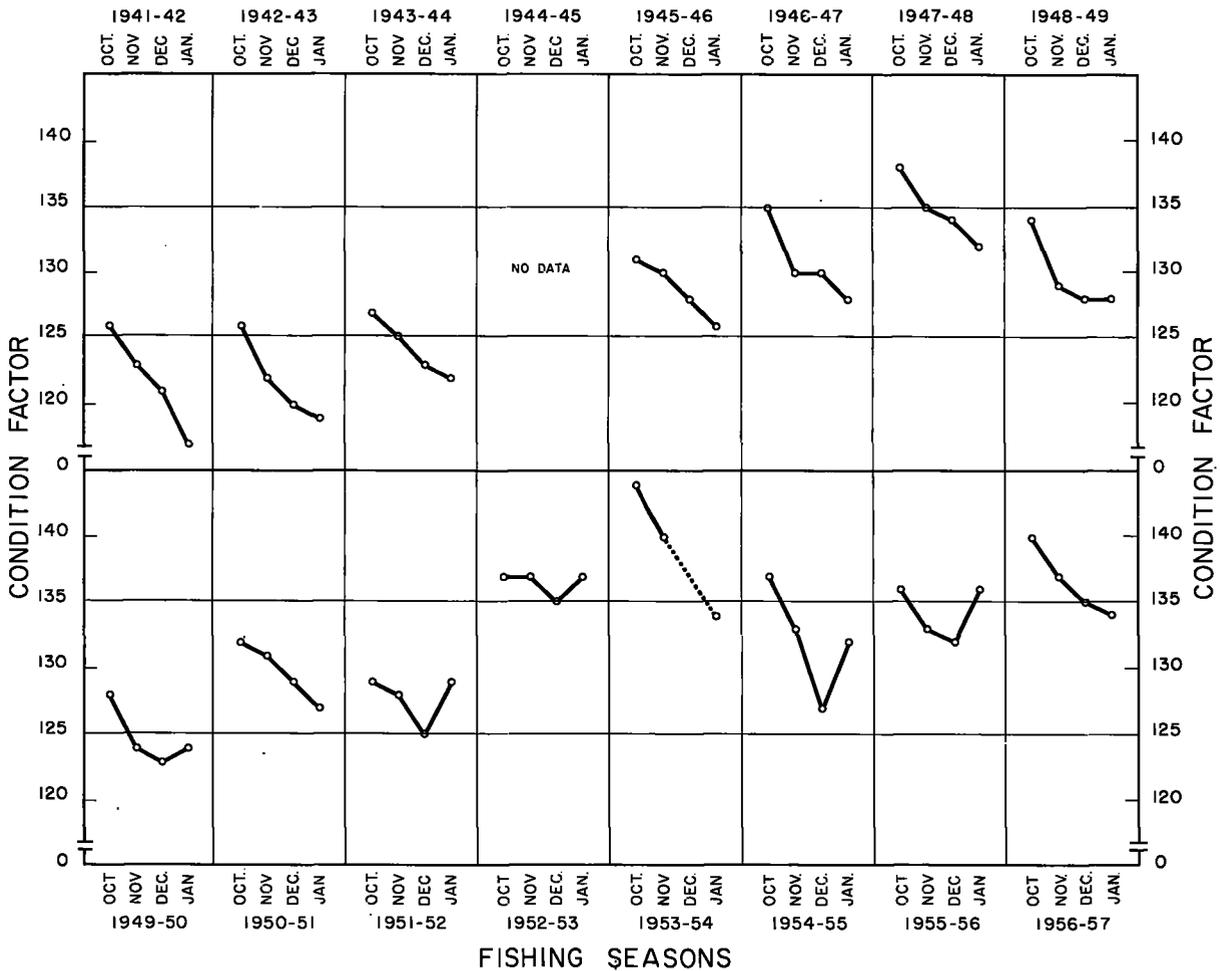


FIGURE 1.—Condition factor trends for San Pedro sardines.

CATCH, LENGTH, AND CONDITION FACTOR RELATIONS

The year-to-year trend of the California sardine catch (thousands of tons) and the inverse trend of the 4-month means of length and condition factor for the 1941-42 through 1956-57 fishing seasons are shown in figure 4. The trends of catch or estimated population in billions of fish and the inverse trends of length and condition factors for any of the 4 months considered separately parallel those in this figure.

Figures 5, 6, and 7 show the least-squares regressions of length and condition factor on each of the three relative measurements of population, and figure 8 shows that of condition factor on length. The regression statistics and other data are given in table 4. All seven associations are significant, but the three relationships involving

condition factor and population have higher correlation coefficients than the three involving length and population.

TABLE 4.—Regression statistics and other data for the regressions of length and condition factor on each of three relative population measurements and of condition factor on length

[Ct = California catch in thousands of tons; Cb = California catch in billions of fish; EP = estimated population in billions of fish; L = length; K = Condition factor.]

X	Y	N	a	b	r	P
Ct.....	L	15	220.165	-.04359	-.788	<.001
Ct.....	K	15	136.188	-.02573	-.903	<.001
Cb.....	L	15	219.952	-5.36347	-.797	<.001
Cb.....	K	15	136.005	-3.13440	-.905	<.001
EP.....	L	14	216.244	-2.05723	-.685	<.01
EP.....	K	14	134.641	-1.37874	-.865	<.001
L.....	K	15	37.667	0.44067	.856	<.001

The regressions involving length are more accurately described by curves than by straight

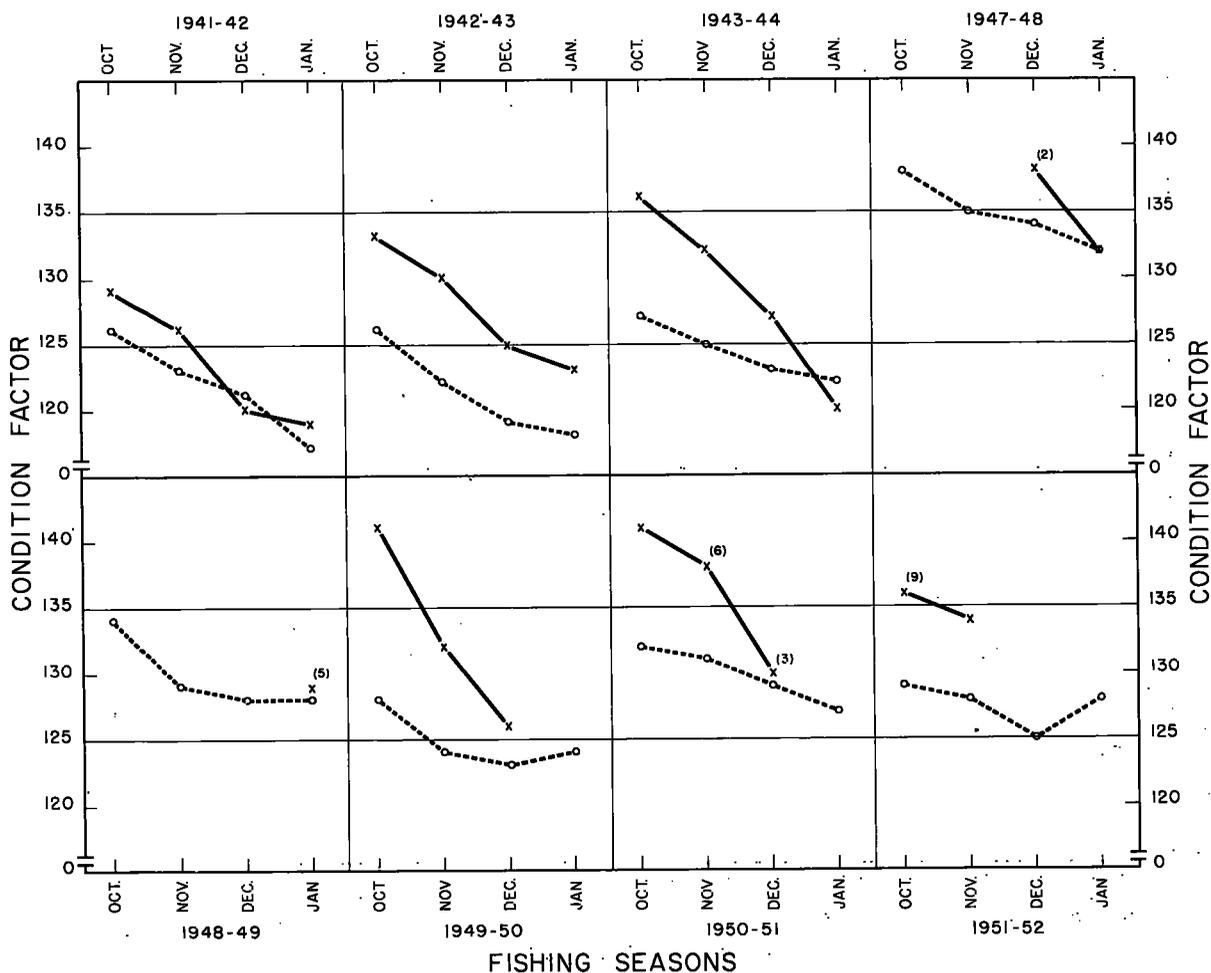


FIGURE 2.—Comparison of San Pedro and Monterey condition factor trends.

lines, even apart from the fact that the lower length limit was arbitrarily taken at 190 mm. For example, in figure 9, the curvilinear regression $Y=193.11+35.08 \left(\frac{1}{X+1} \right)$ fits the plots of length (Y) on catch in billions of fish (X) better than the rectilinear regression $Y=219.95-5.363X$ and the coefficient of correlation is increased from 0.797 to 0.907. However, the rectilinear regression demonstrates the existence of a significant correlation, which is sufficient for the present purposes.

The length and condition factor data taken for each month separately also show high degrees of correlation with one another and with the three relative population measurements.

It now remains to be determined which of the above groups of correlations may represent cause

and effect and which are probably parallel or accompanying phenomena.

DISCUSSION

One result of intensive fishing of a stock of marine fishes is often decreased catch accompanied by decreased fish size (length). In the sardine data, decreases in catch under intensive fishing are accompanied by increases in average fish length, and increases in catch are accompanied by decreases in average fish length. The reasons for this appear to result from the interaction of two factors: (1) any year-class of sardines contributes by far the greatest tonnage to the fishery in its third and fourth years of life (i.e., fish whose scales show, respectively, 2 and 3 annual growth rings), and (2) strength of year-classes fluctuates greatly

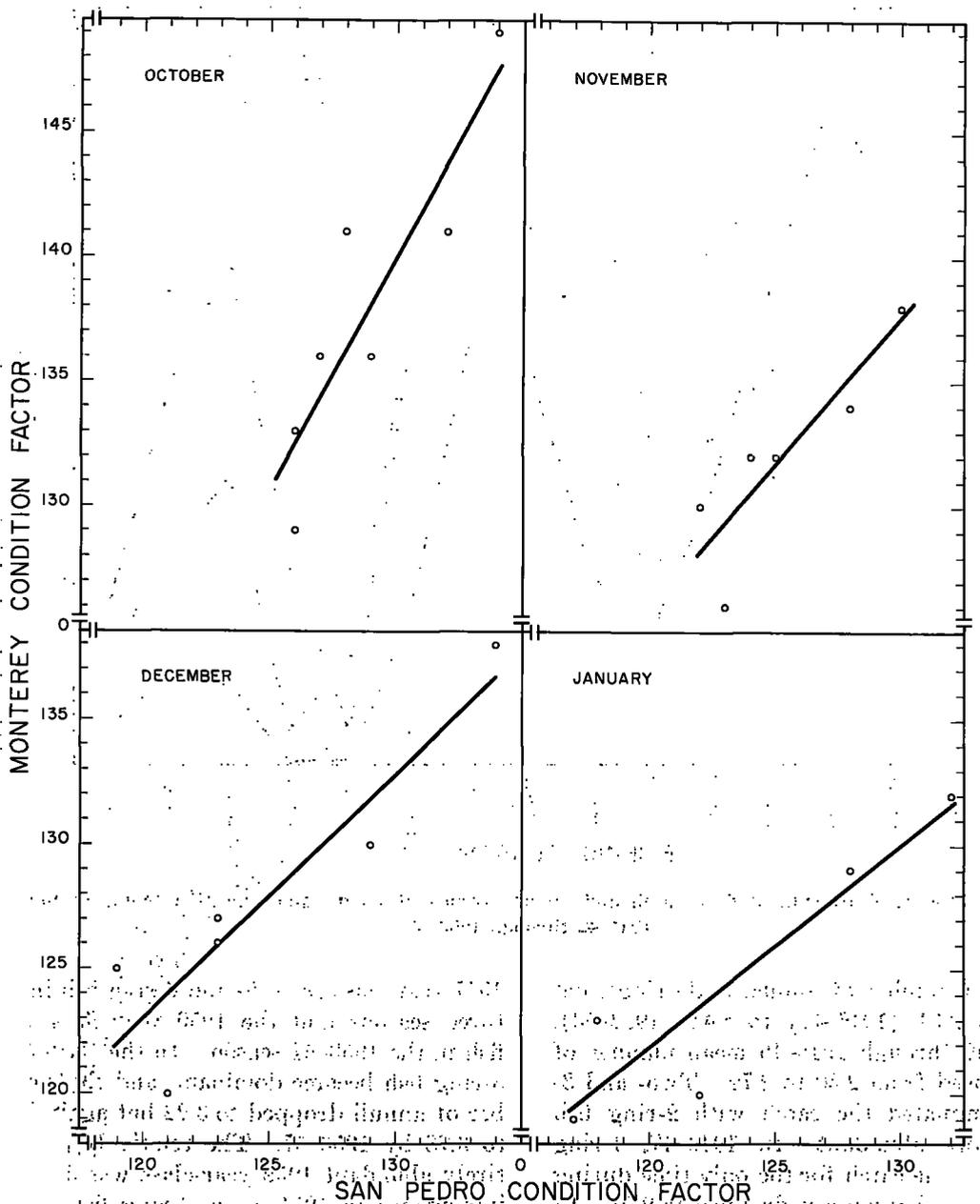


FIGURE 3.—Regressions of Monterey on San Pedro condition factors by months.

from year to year. Thus, the large catches are associated with large year-classes of fish in their third and fourth years of life. These fish are relatively small. On the other hand, small catches are associated with small year-classes in their third and fourth years, together with relatively high percentages of larger, older fish from some former large year-class. According to data presented by Clark and Marr (1955), which

covers the period 1932-33 through 1952-53, the size of the year-class entering the fishery (as 2-ring fish) has averaged 91 percent of the adult population size to which it has been added, and has ranged from 10 percent (1949 year-class in the 1951-52 season) to 286 percent (1946 year-class in the 1948-49 season).

In the 16-season period (1941-42) through 1956-57) the sardine age at San Pedro, as meas-

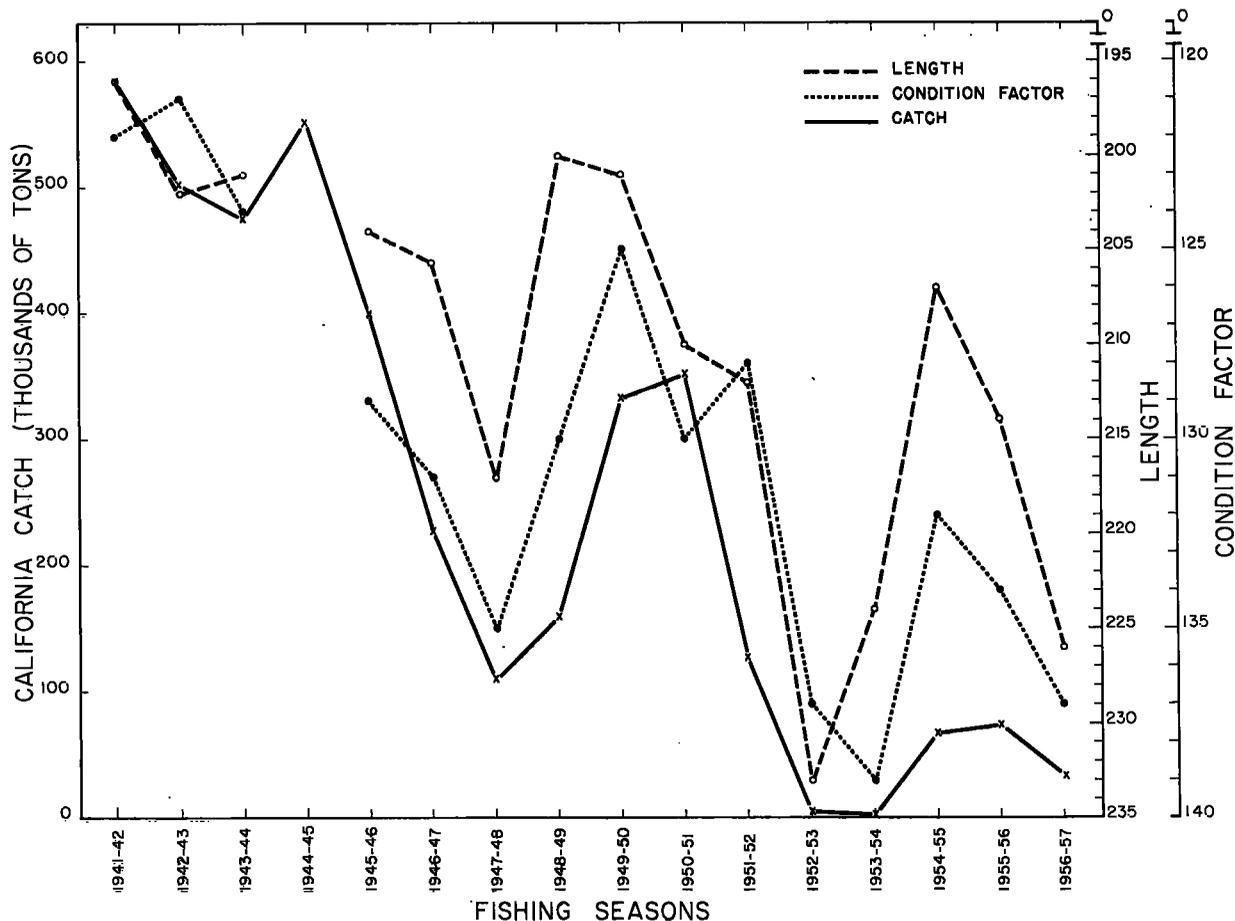


FIGURE 4.—Trend of California sardine catch and inverse trends of length and condition factor at San Pedro 1941-42 through 1956-57.

ured by mean number of annual scale rings, has ranged from 2.01 (1946-47) to 4.41 (1952-53). From 1941-42 through 1945-46 mean number of annuli increased from 2.30 to 2.72. Two- and 3-ring fish dominated the catch with 2-ring fish generally more abundant. In 1946-47, 1-ring fish dominated the catch for the only time during the 16 seasons and mean age dropped to 2.01. In the following four seasons it again increased to 2.73, and during this time 2-ring fish again dominated the catch. From 1950-51 through 1952-53 the mean number of annuli increased from 2.73 to 4.41 and dropped slightly to 4.21 in the 1953-54 season. During these four seasons the 1948 year-class dominated the catch as 2-, 3-, 4-, and 5-ring fish, respectively. This was caused by the almost complete failure of the 1949, 1950 and 1951 year-classes.

Of secondary importance were sardines in the

1947 year-class as 4-, 5- and 6-ring fish in the first three seasons and the 1950 year-class as 3-ring fish in the 1953-54 season. In the 1954-55 season 3-ring fish became dominant, and the mean number of annuli dropped to 3.22 but again increased to 3.78 by 1956-57. The relatively, but not entirely abundant 1952 year-class was of secondary importance in 1954-55 as 2-ring fish, and dominated the catch in the two following seasons as 3- and 4-ring fish, respectively. In the 1956-57 season the persistent 1948 year-class was fourth in abundance as 8-ring fish. During the first 10 seasons (1941-42 through 1950-51) of the 16-year period the California sardine catch averaged 2.90 billions of fish and ranged from 0.93 billions to 5.34 billions; the mean number of annuli averaged 2.46 and ranged from 2.01 to 2.73. During the next six seasons (1951-52) through 1956-57), the catch averaged 0.37 billions and ranged from 0.02

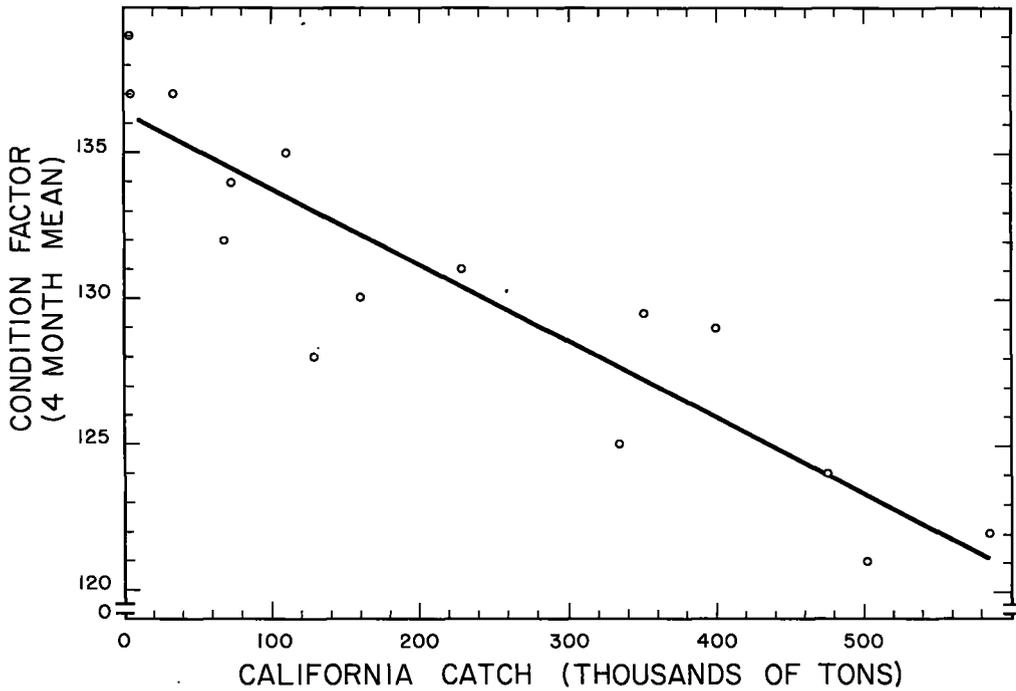
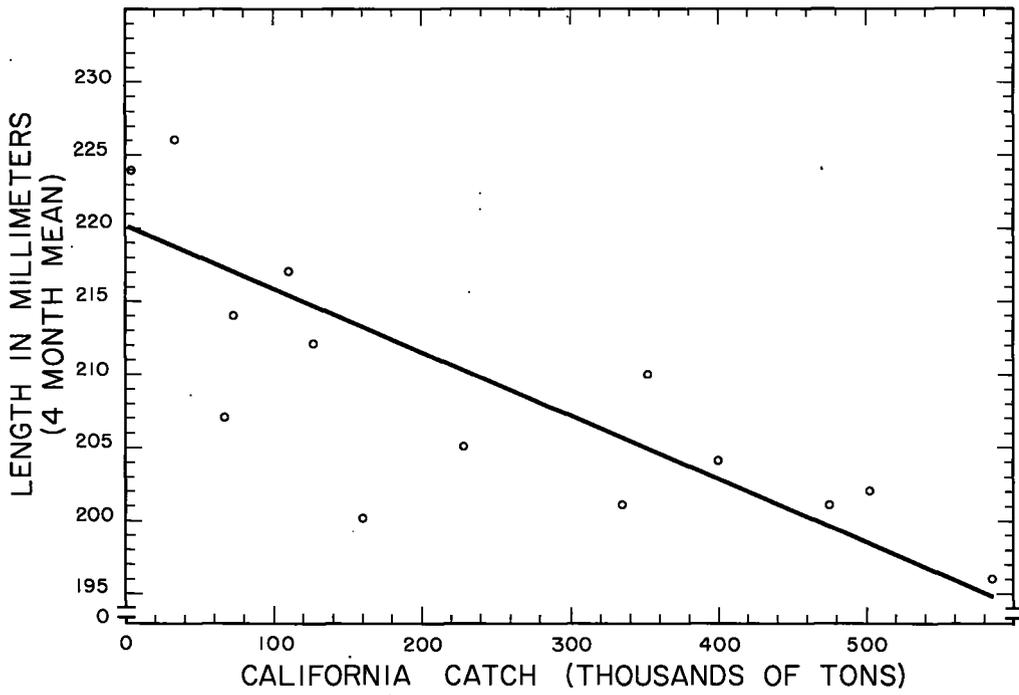


FIGURE 5.—Regressions of length and condition factor at San Pedro on California catch in thousands of tons.

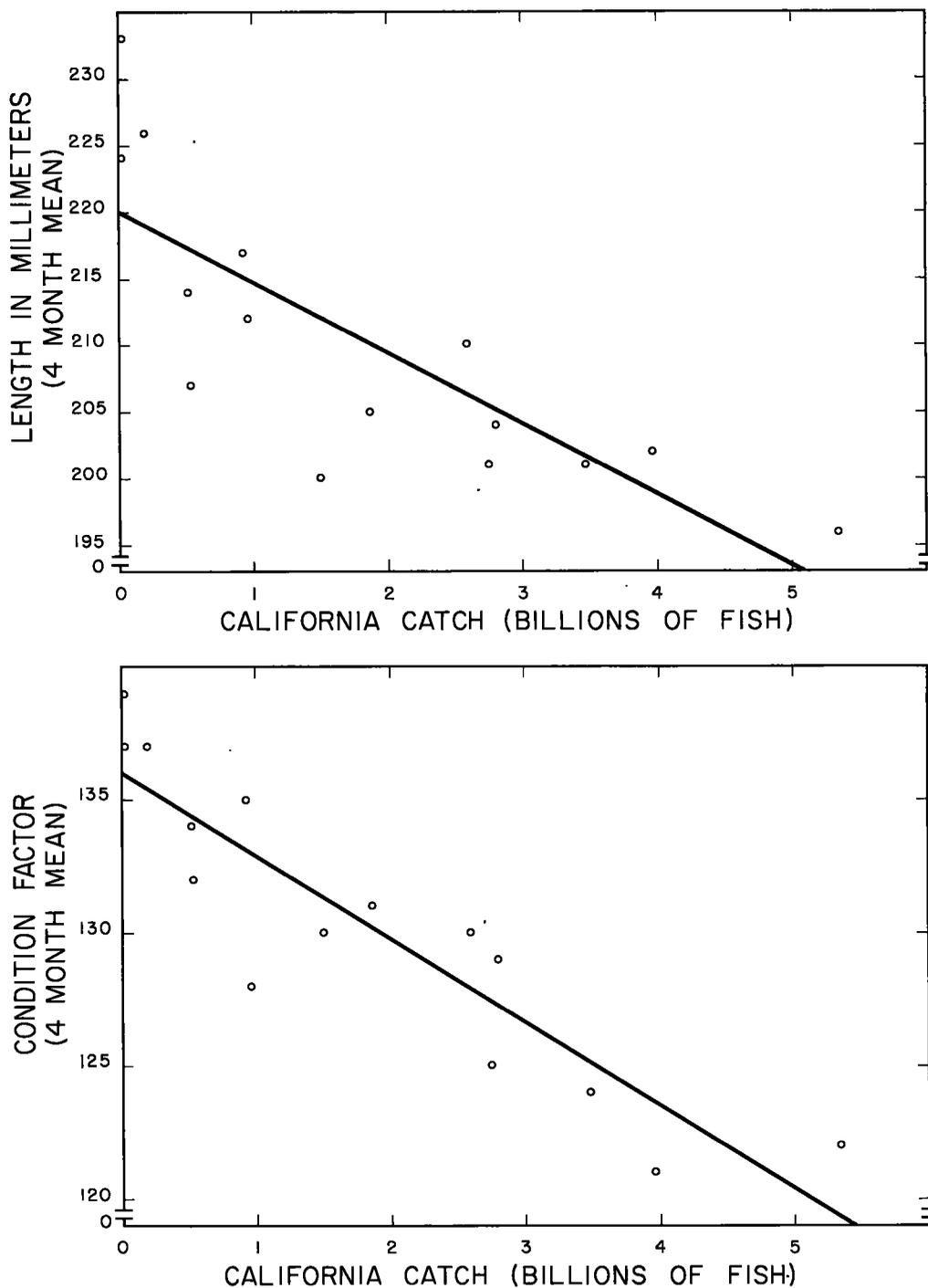


FIGURE 6.—Regressions of length and condition factor at San Pedro on California catch in billions of fish.

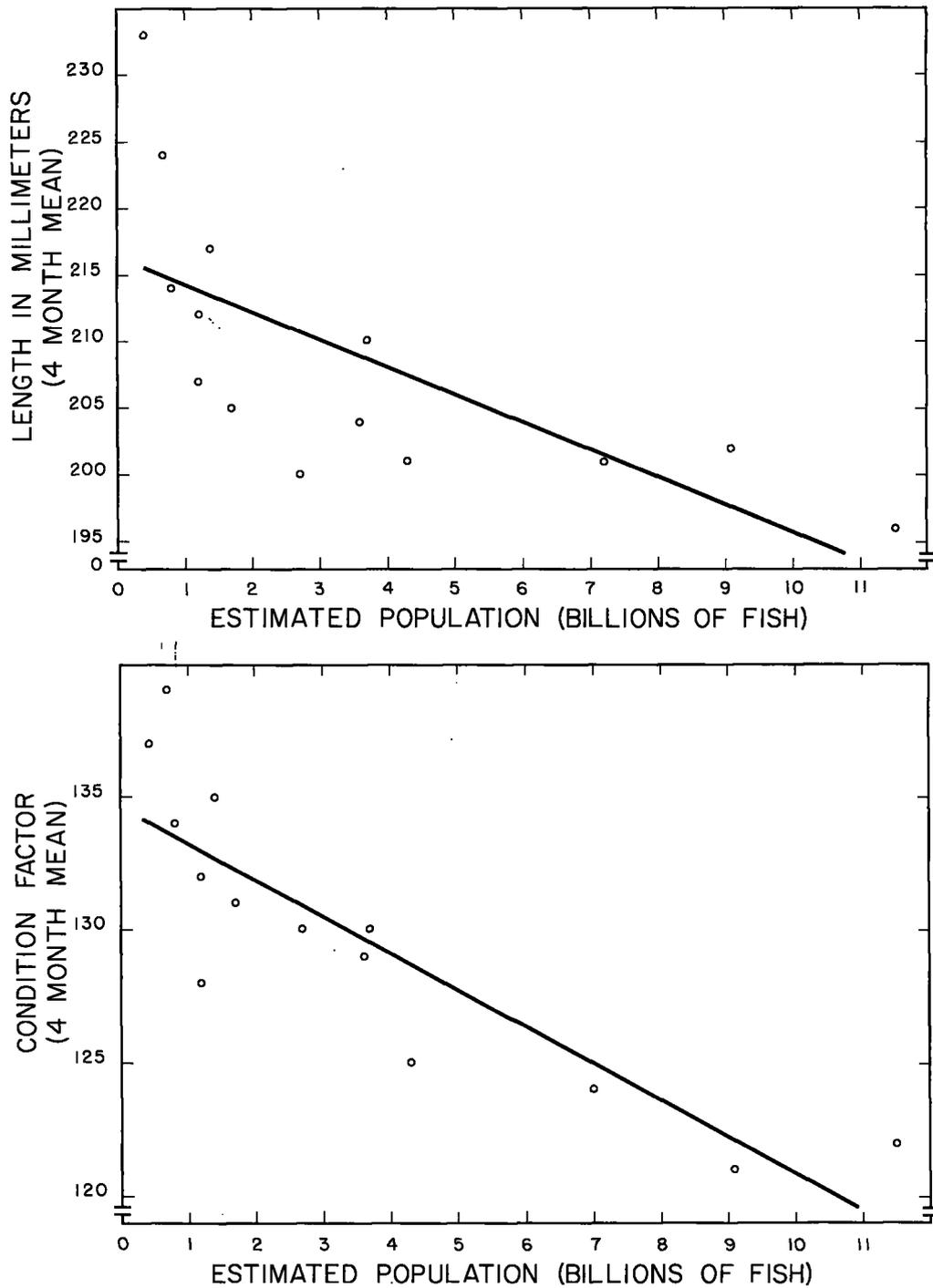


FIGURE 7.—Regressions of length and condition factor at San Pedro on estimated sardine population in billions of fish.

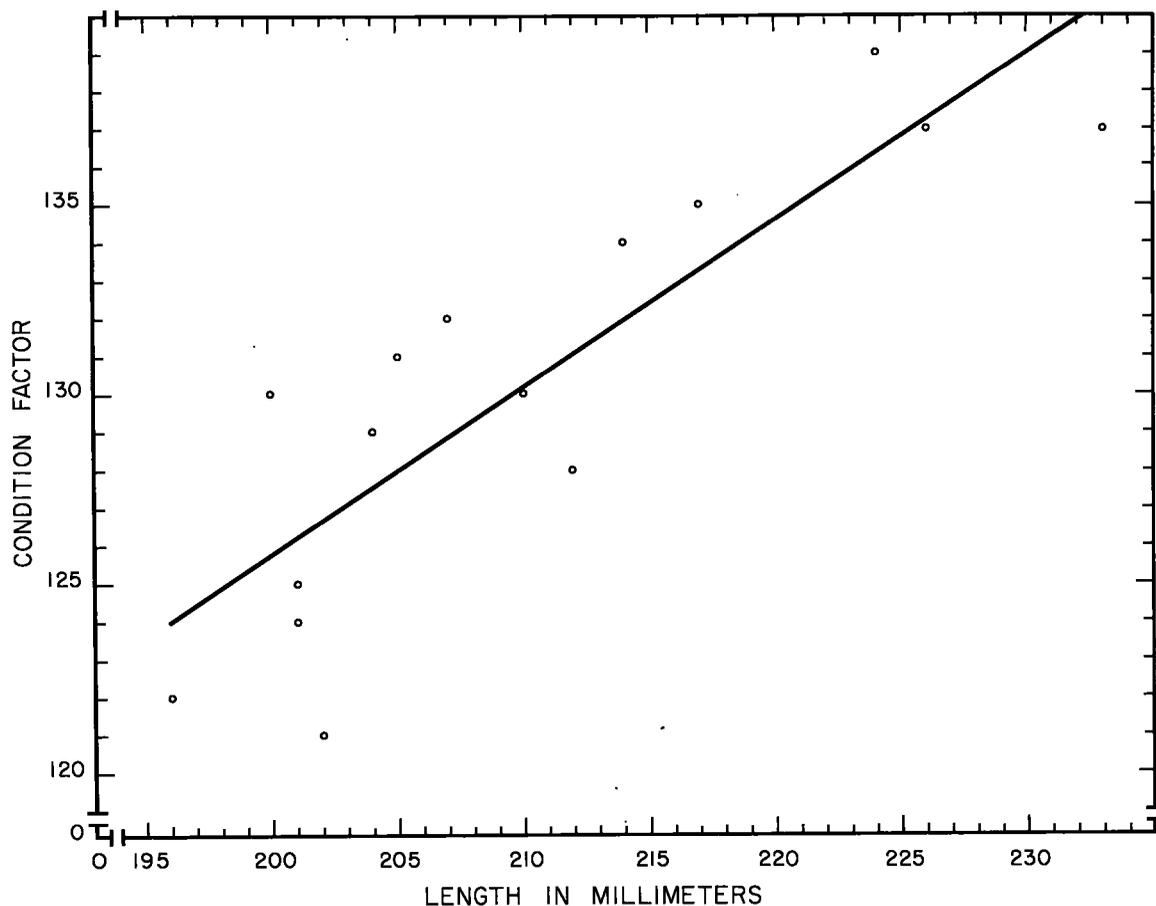


FIGURE 8.—Regression of condition factor on length (October through January means at San Pedro for seasons 1941-42 through 1956-57).

billions to 0.96 billions; mean number of annuli averaged 3.71 and ranged from 3.22 to 4.41.

The lack of direct correlation between condition factor and length is demonstrated by the data in table 5. When the means of K and length for January of each of the 15 years are correlated r is high and P is less than 0.001, but when K and length are correlated for the individual samples for January of each of the 15 years, r is generally low and P is high. By using the data for a single month, errors arising from the seasonal K trends are minimized. Data from any of the other 3 months gives similar results. The data for the years 1954 and 1955 are meaningless because N is too small and the length range is too restricted. N is also too small to have significance in the year 1953.

The fact that 12 out of 15 of the correlation coefficients have a positive value might indicate

TABLE 5.—Correlation of condition factor and length for each of 15 seasons (by individual samples) and seasons combined (mean values) for the month of January at San Pedro

Season (January)	Length range		N	r	P
	Minimum	Maximum			
	<i>mm.</i>	<i>mm.</i>			
1942.....	190	210	46	-.217	>>> 1
1943.....	190	214	48	.183	>>> 1
1944.....	190	225	47	.321	.05 >>> .02
1946.....	193	220	20	.232	>>> 1
1947.....	198	227	14	.000	>>> 1
1948.....	204	231	9	.304	>>> 1
1949.....	191	211	12	.050	>>> 1
1950.....	194	213	13	.675	.02 >>> .01
1951.....	208	231	30	.173	>>> 1
1952.....	202	234	21	.194	>>> 1
1953.....	228	239	5	.278	>>> 1
1954.....	221	222	3	.316	>>> 1
1955.....	208	209	3	-.316	>>> 1
1956.....	210	220	11	.070	>>> 1
1957.....	221	232	9	.770	.02 >>> .01
11 years.....	196	233	15 (means)	.858	<<< .001

that there is a slight tendency for K to increase with length, but this could also arise from other causes. For example, there appears to be a tend-

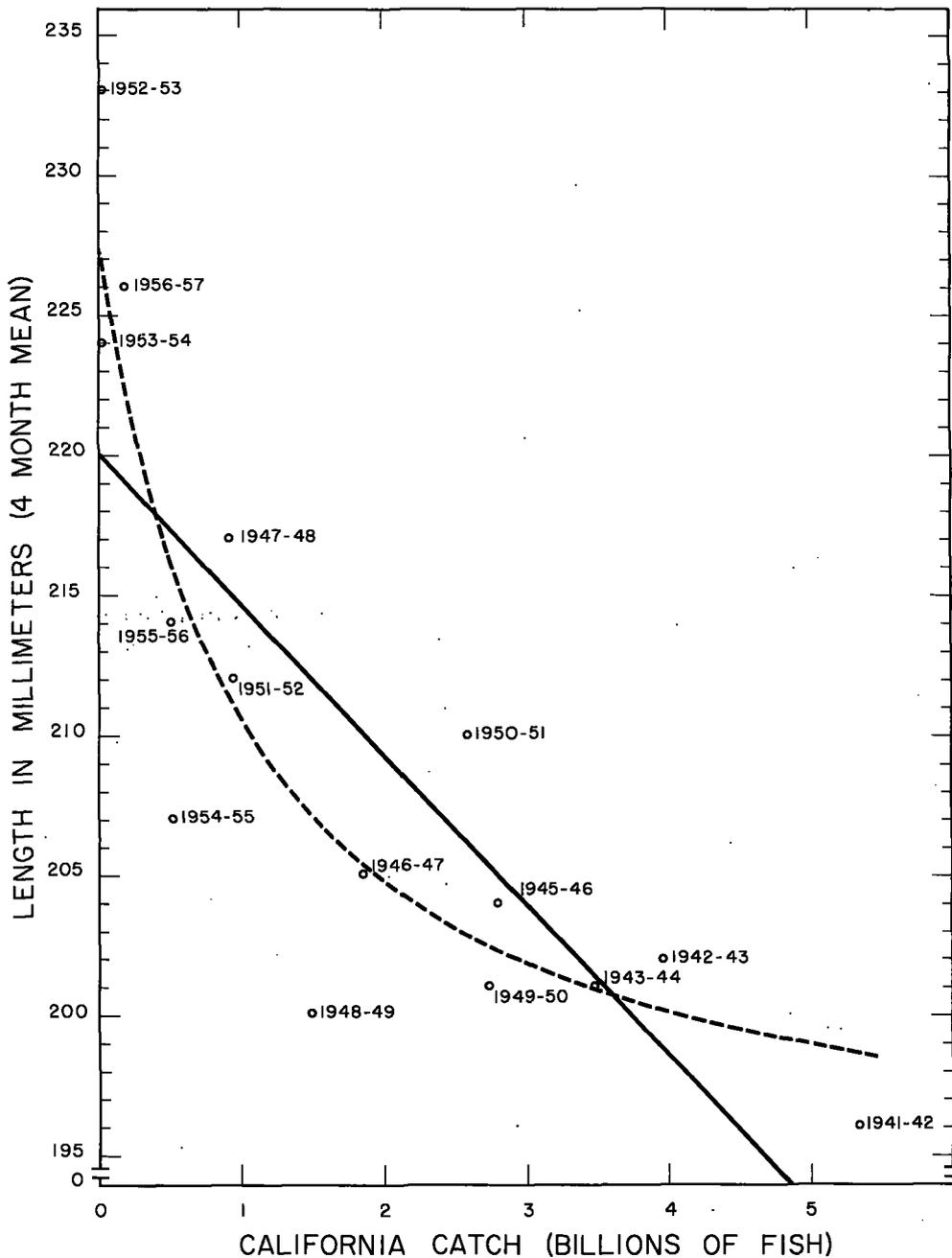


FIGURE 9.—Comparison of curvilinear and rectilinear regressions of mean length of San Pedro sardines on California catch in billions of fish. Solid line: $Y=219.95-5363X$, $r=.797$; dashed line: $Y=193.11+35.08\left(\frac{1}{X+1}\right)$, $r=.907$.

ency for the sardine population off the California coast to move southward during the course of the fishing season, and there is also a tendency for the more northern fish to be of larger size. However, this does not explain the highly significant correla-

tion of K and the length for all years, or the general lack of significance for the individual years. Mean length is strongly influenced by the size of the last large year-class, which in turn determines in large measure the population size

(as measured by catch). Also, condition factor is apparently determined to a considerable degree by population size, and hence, there has been, over the 15-year period, an apparent correlation between length and K . That this correlation is of a parallel nature rather than cause and effect is in agreement with Clark's (1928, 1934) findings that the weight-length relationships of the sardine closely approximate the cubic form.

Table 6 presents the data illustrating the correlation of California sardine catch and K for January at San Pedro for the years 1942 through 1947. The data include the means for all fish and for each of the five 10-mm. length groups observed during the period. The value of r is high in each of the six groups and P is greater than 0.001 only in those two in which N is very low. This constitutes additional evidence that changes in K are probably associated with population size, and not length.

It is probable that the growth rate in terms of length is also greater for the sardine in times of low population density than in times of high population density. Of the 15 year-classes 1939 through 1952, five averaged less than 200 mm. in length as 2-ring fish. The estimated size of these five year-classes (1939, 1940, 1941, 1946, and 1947) (Clark and Marr, 1955) ranged from 1.9 billion fish to 7.2 billion fish and averaged 3.34 billion fish. Ten-year-classes averaged 200 mm. or larger as 2-ring fish. Seven of these year-classes ranged in estimated size from 0.1 to 2.3 billion fish and averaged 1.04 billion fish. Data for the other three year-classes (1951, 1952, and 1953) are incomplete, but they were well within the range of the other seven and would not markedly affect the average.

There are several complicating factors in the apparent association between year-class size and length growth. The size of the remaining population is not taken into account. Also, length reflects cumulative growing conditions over the life of the fish, while the condition factor more closely reflects current conditions. A year-class originating primarily in Sebastian-Viscaino Bay off Baja California probably has a different growth pattern than one originating off southern California, and one originating from a peak March spawning probably has a different growth pattern than one originating from a peak June spawning.

TABLE 6.—Correlation data for condition factor (by length groups) at San Pedro in January and California sardine catch (thousands of tons) for the years 1942-57

Length group	N	r	P
190-199	7	-.859	.02 > .01
200-209	11	-.913	< .001
210-219	10	-.846	< .001
220-229	9	-.946	< .001
230-239	4	-.972	.05 > .02
All lengths	15	-.954	< .001

¹ Each K value is a mean of all January samples for that year.

One possible explanation of the high degree of inverse correlation between population size, as measured by the California catch, and condition factor is that there is a southward shift of the entire population (possibly owing to hydrographic conditions) in years of small population and a northward shift during years of large population. The data of figure 2 shows that the condition factors at Monterey tend to run higher than at San Pedro. However, the high degree of inverse correlation between catch and condition factor for January, when Monterey and San Pedro condition factors tend to be most nearly the same, does not substantiate this hypothesis.

Although the range of the California sardine extends farther to the north in years of large population and contracts toward the south in years of small population, sardine schools are not uniformly distributed throughout their range. During good years the population density is much greater within the range, also seasonal concentrations of schools occur within the range. Although the range of the sardine is bounded by land only on the east, it is probable that it is also bounded on the other sides by oceanographic features, so that as population size increases, within-range density increases more rapidly than the total range. Therefore, the inverse correlation of K and population (as measured by catch) could result from less available food-per-fish in times of large population and vice versa if the total amount of food available within the area did not vary considerably from year to year. If this hypothesis is true, it implies that the adult sardines have little interspecific competition for food.

Other similar-sized schooling species whose ranges overlap that of the sardine in California waters are the anchovy (*Engraulis mordax*), the Pacific mackerel (*Pneumatophorus diego*) and the jack mackerel (*Trachurus symmetricus*).

Anchovies have been abundant during the past few years, while the sardine population has been small. To a certain extent anchovies tend to frequent areas where sardines are not present and vice versa, although they are sometimes found schooling together. The largest anchovy catch in the years 1916 through 1955 occurred in 1953, when 43 thousand tons were taken by the commercial fishery and 6,000 tons by the live-bait fishery (Miller 1956). The anchovy stock is not fished intensively.

Landings of jack mackerel reached a peak of 67,000 tons in 1950 (Fitch 1956a). The population is probably not being intensively exploited by the fishery. Both the anchovy and jack mackerel were not fished to any great degree until the decline of the sardine population caused these two species to be sought as substitutes for canning purposes.

The Pacific mackerel has been intensively fished off the California coast over the 1940-41 to 1956-57 period covered by the sardine data. The highest catch in this period was 54,000 tons in the 1940-41 season (Fitch 1956b), although higher tonnages were landed in two seasons in the previous decade. Large year-classes of Pacific mackerel seem to have a slight tendency to coincide with large year-classes of sardines.

The anchovy appears to be a filter-feeder, whereas the two mackerels are selective feeders. Fitch (1956a) found that jack mackerel feed to a large extent on small crustaceans and also at times on juvenile squid and anchovies. Fitch (1956b) also stated that examination of 228 Pacific mackerel stomachs revealed that they feed largely on larval and juvenile fish and small crustaceans.

Lewis (1929) stated that the sardine is a filter-feeder, but Radovich (1952) concluded that it is also a particulate feeder. He found one occurrence of sardines feeding on juvenile anchovies. Sardines kept in tanks or large aquaria have been observed feeding selectively on numerous occasions.

Nothing is known about interspecific food competition between the adult anchovy and sardine. There is probably competition between the mackerels and the sardine as, in fact, they are not in-

frequently found in mixed schools and, at times, apparently feeding on much the same types of organisms. However, very little information is available on food competition among these and other local marine species, and such relationships must remain a matter of conjecture for the present, at least. A second way in which population size might affect feeding and condition factor is by its effect on school size. Large populations could result in large schools and smaller populations in smaller schools. It seems logical that a small school could feed more efficiently per individual fish than a large school.

SUMMARY

Low population levels of the Pacific sardine (*Sardinops caerulea*) (as indicated by the California catch) are associated with higher condition factors and greater average lengths of these fish and, conversely, high population levels are associated with lower condition factors and smaller average lengths.

The high degree of inverse correlation between population size and condition factor is interpreted as a cause and effect relation; that is, high population levels result in less available food-per-fish and lower condition factors, while low population levels result in more available food-per-fish and higher condition factors.

The inverse correlation between population size and fish length appears to result from the entrance of large year-classes into the population. When this occurs, average size (and age) is reduced as population size is increased. When small year-classes enter the population, average size (and age) is increased (because of the relatively high proportion of large, old fish in the population) as population size is decreased.

The apparent positive correlation between condition factor and length over the 15 seasons is not of a cause and effect type, but rather a parallel phenomenon. In years when high condition factors prevailed, all fish had high condition factors regardless of size and, conversely, in years when condition factors were low, all fish had low condition factors regardless of size.

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ESTIMATES OF LARVAL TUNA ABUNDANCE IN THE CENTRAL PACIFIC

BY DONALD W. STRASBURG



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ABSTRACT

Certain aspects of larval tuna sampling were studied by an analysis of the catches of the 0, 0-60, 70-130, 140-200, and 0-200 meter plankton tows made on 15 cruises in Hawaii, the equatorial Pacific, and French Oceania. The use of paired nets showed that the catch of a single net could be duplicated, and that plankton nets were therefore reliable tools for sampling the abundance of tuna larvae.

Most larval tuna were captured between the surface and 60 meters, with 20-25 percent more between 70 and 130 m., and practically none between 140 and 200 m. Marked night-day differences in catch occurred at the surface but became less at greater depths. Most of these differences were attributable to vertical migration rather than net-dodging. The 0-200 m. tow, fishing through the entire depth range of larval tuna, was regarded as the best of the tows tested.

Larval skipjack and frigate mackerel were rarely captured during the day by the 0 and 0-60 m. tows, but this was not true for yellowfin. Both skipjack and yellowfin began to appear at the surface in the afternoon but disappeared at sunset, to reappear somewhat later. This disappearance from the surface was correlated with the rise of the deep scattering layer.

The dominant size group in the larval tuna catch measured from 4.0-4.9 mm. total length. Many larvae of 2.0-2.9 mm. total length were presumed to have escaped through the net meshes, while larvae longer than 5 mm. may have escaped by dodging.

No significant relations were found between the numbers of adult yellowfin and skipjack and their respective larvae.

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BUREAU OF COMMERCIAL FISHERIES

For the past several years the Pacific Oceanic Fishery Investigations (POFI), of the U. S. Fish and Wildlife Service, has sampled adult tuna stocks as a means of evaluating the tuna resources of the central Pacific Ocean. Deep-swimming tunas, such as large yellowfin (*Neothunnus macropterus*), bigeye (*Parathunnus sibi*), and albacore (*Germa alabunga*), were taken by longlining, and surface dwelling tunas, such as skipjack (*Katsuwonus pelamis*), and small yellowfin and albacore, have been captured by live-bait fishing, gillnetting, and trolling. The catches obtained by these methods were used as indices of the availability, distribution, and abundance of the tuna, and the biological studies of adult fish contributed information on reproductive cycles, food habits, growth rates, and other phenomena.

For some of the above operations, good fishing localities could frequently be judged by the presence of sea birds, knowledge of the circulation features, water of a certain color or temperature, or other factors, but in the absence of such guides, fishing sites were more or less randomly selected. In areas where sea birds were scarce or absent, such as a large part of the open ocean, our knowledge of surface tuna abundance was scanty, thus raising the question of the reliability of the several guides. Another inadequacy of the sampling method was that running ripe fish were rarely caught, either because of their migration from the fishing grounds, cessation of feeding during spawning, or the breaking up of schools during the reproductive period. There was little precise information, therefore, on the time and place of spawning except for the general trends evident from gonadal studies.

It was believed that a study of the eggs, larvae, and juveniles of tuna would be of considerable aid in filling certain gaps in our knowledge. The

occurrence of eggs and larvae, as collected in plankton tows, should indicate the recent or continuing presence of adult fish independently of external indicators, and should prescribe the time and place of spawning with accuracy, depending on current drift and ontogenetic age. With reliable estimates of abundance, it should be possible to determine the numerical relations between adult tuna, their eggs, and larvae.

Before these major problems could be studied effectively it was necessary to consider the sampling methods employed. Among other things, it was requisite to know the reliability of a plankton tow as a method of capturing tuna eggs and larvae, and also to standardize the time and depth of tow so that meaningful comparisons could be made between samples. Because of its occasionally profound effect on the catch, it was desirable to understand the rudiments of larval tuna behavior. A study of these problems resulted in the present report, but because tuna eggs are not presently identifiable, its scope is limited to larval and juvenile forms. I should like to express my gratitude to Walter Matsumoto for his help in identifying tuna larvae, and to other POFI staff members who aided in collecting and processing the samples and in reviewing the manuscript.

METHODS

Collecting

All larvae reported upon were collected by plankton tows made from the POFI vessels *Hugh M. Smith* and *Charles H. Gilbert*. Three cruises were limited to the Hawaiian area, and 12 took place in the equatorial Pacific with some emphasis on the waters of French Oceania. Matsumoto (1958) has already presented data for 8 of these 15 cruises (*Hugh M. Smith* cruises 5, 6, 7, 8, 11, 14, 15, and 18). The operational areas of the remaining 7 cruises are shown in figure 1, and appendix tables 5 through 11 summarize catch and effort for each station.

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POFI was redesignated Bureau of Commercial Fisheries Laboratory, Jan. 1, 1959.

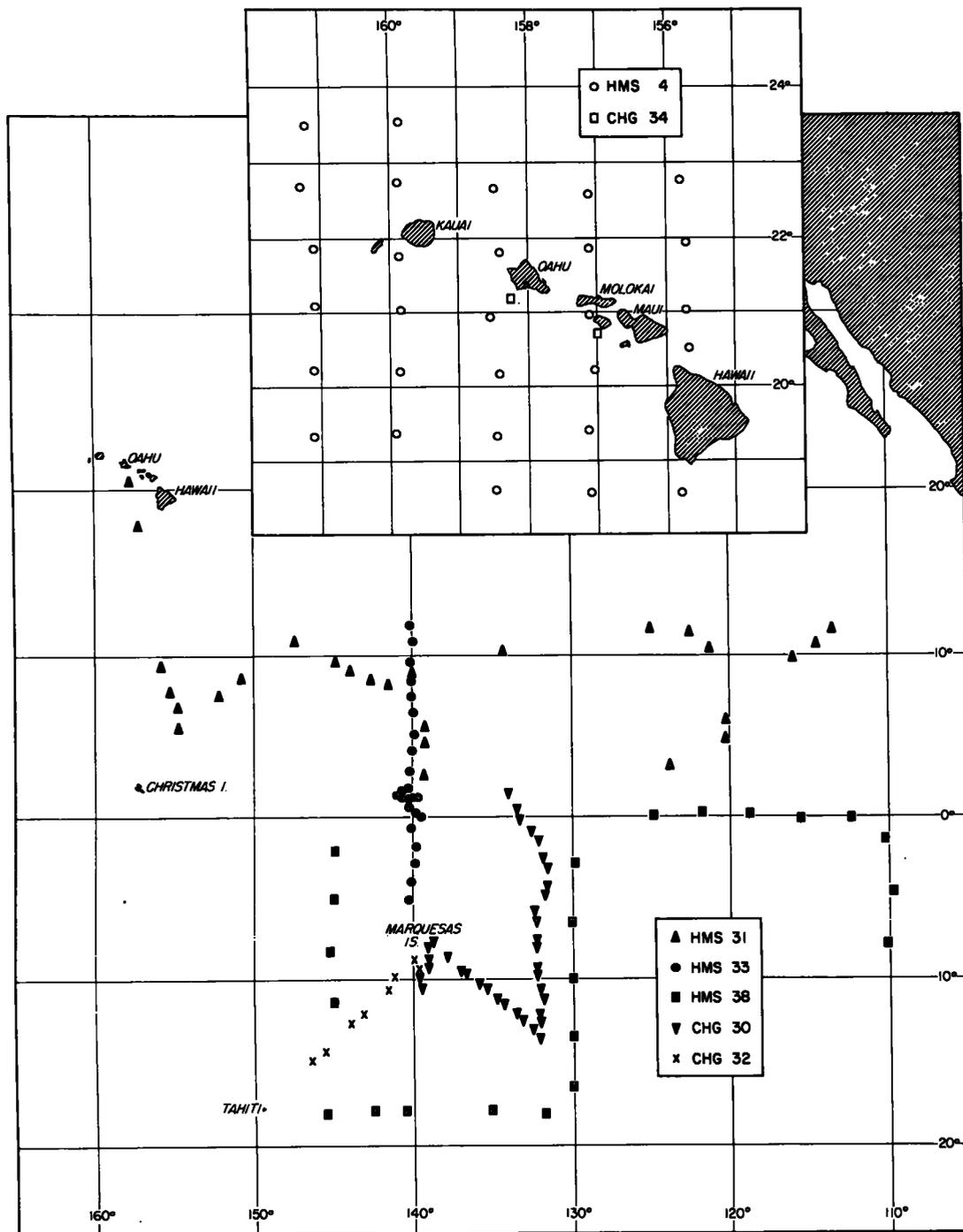


FIGURE 1.—Plankton stations sampled for larval tunas.
 HMS=Hugh M. Smith, CHG=Charles H. Gilbert.

All plankton nets employed were 1 meter diameter at the mouth and 5 meters in length. The nets were of two types, open and closing, the structural details of which are given by King and Demond (1953) and King and others (1957). On early cruises the nets were fabricated of Dufours bolting silk or silk grit gauze (30XXX body and 56XXX rear section), but these materials were later replaced by nylon (#656 Nitex body and #308 Nitex rear section); for all nets, mesh apertures were 0.66 mm. in width in the body and 0.31 mm. in the rear section and bag. The nets were equipped with flowmeters to measure the amount of water strained.

Three types of plankton tows were made: horizontal open net tows, oblique open net tows, and oblique closing net tows. For this study only those horizontal open net tows which fished at the surface were considered, and these can be termed simply surface or 0-meter tows. They fished just deeply enough so that the nets did not break the surface. Oblique open net tows were made from the surface to about 60 m. and from the surface to about 200 m.; for brevity these are designated as 0-60 m. and 0-200 m. tows. The oblique closing net tows involved a string of three nets, the upper one being an open net fishing from the surface to approximately 60 m., the middle a closing net fishing from about 70 to 130 m., and the lower a closing net fishing from about 140 to 200 m. These are designated as 0-60 m., 70-130 m., and 140-200 m. tows, with the first being indistinguishable from the 0-60 m. oblique open net tow. Ordinarily, tows were 1/2-hour in duration, but some were as short as 15 minutes or as long as 1 hour, at towing speeds of 2.5 to 3.5 knots.

Processing

At the completion of each tow the nets were hauled aboard, hosed down to remove plankton residues, and the samples transferred to glass fruit jars and preserved in 10-percent borax-neutralized formalin. As soon as possible after returning to the laboratory all fish and fish eggs were removed, and, from these, all young tuna were sorted and transferred to clean formalin for storage.

Identification

Larval tuna were identified principally with reference to Matsumoto's two recent papers

(Matsumoto 1958 and 1959). POFI's extensive collections provided comparative material, and in some cases Matsumoto examined the specimens. The vast majority of specimens were referable to skipjack (*Katsuwonus pelamis*), yellowfin (*Neothunnus macropterus*), frigate mackerel (*Auwis thazard* and *Auwis* sp.), and little tunny (*Enthynnus yaito*); these are designated by their common names throughout the balance of this report. Of the unidentified material, a few specimens belonged to species for which the larvae are undetermined, and the remainder were severely mutilated.

Terminology

Larva denotes a specimen lacking the full complement of vertical fin spines and rays. This term includes most individuals below about 11 mm. in total length.

Length is total length, measured from the tip of the snout to the end of the longest caudal ray; where the caudal is forked, length is fork length.

Abundance is expressed as the number of larvae per thousand cubic meters of water strained, and also as the number of larvae beneath 10 square meters of sea surface.

Time is expressed in terms of the 24-hour clock, with zone time being used in each case.

Invertebrate plankton volume is the displacement volume measured subsequent to the removal of all fish, fish eggs, and organisms larger than 5 cm. longest dimension.

RELIABILITY OF A SINGLE SAMPLE

It was reasoned that if the catch made by one plankton net could be duplicated by another fishing at the same time and place, then plankton nets are reliable tools for sampling larval tuna within certain limitations of the sampling method. Reliability was first tested on *Charles H. Gilbert* cruise 30 to the Marquesas Islands. Two surface nets were launched simultaneously at 2000 hours each night; they fished about 20 feet apart for one-half hour after which they were retrieved, rinsed, the cod-ends replaced, and the procedure repeated for a second half-hour. Fourteen stations, each including a 4-haul series, were occupied, but the sampling was apparently done in the off-season (Aug.-Sept.) with respect to Marquesan tuna spawning, and few larvae were col-

lected. A second test was made during January-March on *Hugh M. Smith* cruise 38 to French Oceania. Here, two half-hour tows were taken each night, one immediately following the other, so that members of a pair of samples differed slightly in time and space. The data obtained

from these tests are listed in detail in the appendix and in summary form in table 1. With respect to the latter, it should be noted that all species of tuna larvae were combined and that only those stations were considered where larvae were taken by one or more nets.

TABLE 1.—Numbers of larval tuna captured by paired night surface tows, with analyses of variance based on transformed data

$$\left[x' = \log \left(\frac{x+1}{10,000m^3} \right) \right]$$

Charles H. Gilbert cruise 30				Hugh M. Smith cruise 38			
Station No.	Position	Time		Station No.	Time		
		First ½ hr.	Second ½ hr.		First ½ hr.	Second ½ hr.	
3	(Port.....)	3	1	23	9	18	
7	(Starboard.....)	1	2	45	2	0	
7	(Port.....)	1	0	47	11	4	
9	(Starboard.....)	1	2	49	0	2	
9	(Port.....)	1	0	54	4	1	
13	(Starboard.....)	0	0	57	7	47	
13	(Port.....)	2	1	59	13	21	
15	(Starboard.....)	1	2	64	2	1	
15	(Port.....)	0	0	66	3	1	
17	(Starboard.....)	1	0	75	2	2	
17	(Port.....)	0	0	79	16	4	
21	(Starboard.....)	0	1	82	56	61	
21	(Port.....)	14	13	85	10	13	
23	(Starboard.....)	17	26				
23	(Port.....)	4	1				
25	(Starboard.....)	2	1				
25	(Port.....)	0	0				
32	(Starboard.....)	2	0				
32	(Port.....)	5	2				
	(Starboard.....)	1	4				

Analysis of variance				Analysis of variance			
Source	Degrees of freedom	Sum of squares	Mean square	Source	Degrees of freedom	Sum of squares	Mean square
Time (T).....	1	0.0185	0.0185	Time.....	1	0.0023	0.0023
Stations (S).....	9	4.5071	**0.5008	Stations.....	12	5.6130	0.4680
Positions (P).....	1	0.0168	0.0168	T×S.....	12	0.9542	0.0795
T×S.....	9	0.1549	0.0172	Total.....	25	6.5725	
T×P.....	1	0.1102	0.1102				
S×P.....	9	0.2258	0.0251				
T×S×P.....	9	0.2540	0.0282				
Total.....	39	5.2873					

**Indicates a significant F value ($p < 0.01$).

A preliminary examination of the data indicated that they were skewed, and this was verified by plotting station variances against station means for the *Charles H. Gilbert* samples (fig. 2). A logarithmic transformation was accordingly performed, using the expression $x' = \log \left(\frac{x+1}{V} \right)$, where V is the volume of water strained in ten-thousand cubic meters. The use of the quantity $(x+1)$ eliminated all zero terms. An analysis of variance was made on the transformed data (table 1). Interaction terms were assumed to be negligible, and were used to test significance.

The analysis of variance produced no significant F -values except for the "stations" category. Because the station interval varied from 90 to 200 miles, significant differences are not surprising, particularly in view of the extended geographical coverage of the two cruises (fig. 1). However, between-station differences are of less interest than are those types of variability leading to errors in estimating spatial and temporal abundance.

It is difficult to conceive of a biological situation leading to statistically different port and starboard catches, for any such differences would

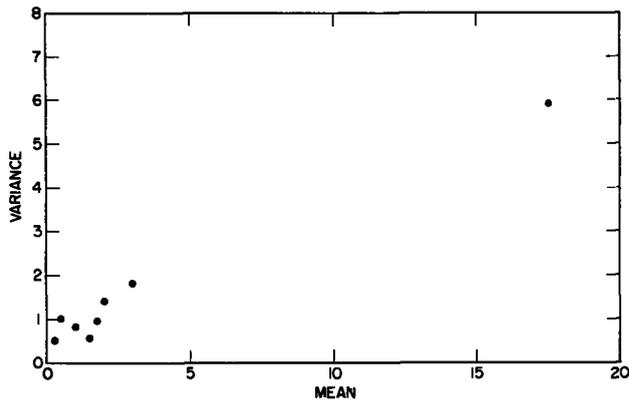


FIGURE 2.—Unadjusted larval tuna catches showing relation between means and variances. Data from surface tows taken on *Charles H. Gilbert* cruise 30 (table 1), stratified by station.

tend to be canceled in random sampling. On an a priori basis one could almost say that the statistical test was unwarranted, but before concluding that the catches of the two nets were duplicates it is well to consider additional information available from table 1. The fact that a logarithmic transformation was necessary implies contagion, or in other words, tuna larvae are not randomly distributed in the ocean. They apparently occur in patches, perhaps resulting from spotty spawning, early attempts to school or form feeding aggregations, or other factors. Under these circumstances a single measurement is not too reliable an estimate of larval abundance. It is possible to set fiducial limits to the catch listed in table 1 by use of the error terms' mean squares, these being estimates of the population parameter, σ^2 . Ninety-five percent (2σ) confidence limits were selected, and these were converted to ratios by use of their antilogs. For the *Charles H. Gilbert* data, the 95-percent limits were 46 percent ($100 \times 1/2.17$) and 217 percent (100×2.17), while for the *Hugh M. Smith* samples the limits were 27 and 366 percent. For one tow to differ significantly from another, its catch would have to be either less than about $1/2$ ($1/4$), or greater than 2 (3) times the catch of the second tow.

No statistical differences were found between samples taken a half-hour apart at night; the subject of a change in catch with the advance of night is discussed later in this report.

VARIATIONS IN THE DISTRIBUTION OF LARVAL TUNA

General Vertical Distribution

Wade (1951) and, more recently, Matsumoto (1958) have demonstrated marked differences in larval tuna abundance between day and night surface catches. Matsumoto suggested that these differences were caused by a vertical diurnal migration of tuna larvae, with the fish rising to the surface at night and descending to depths probably not greater than 50 meters during the day. In addition to vertical migration, this diurnal variation in the catch could also be produced by the larvae dodging the net. Larvae should be able to see an approaching plankton net more clearly during the day than at night.

In order to compare the relative importance of migration and dodging in larval tuna sampling, a study was made of the night and day catches of nets fishing at several depths. The data for all species of tuna larvae were pooled, and an average catch was calculated from all available samples (*Hugh M. Smith* cruises 4, 5, 6, 7, 8, 11, 14, 15, 18, 31, 33, and 38; *Charles H. Gilbert* cruises 30, 32, and 34). The data were derived principally from samples containing at least one tuna larva, as it was reasoned that the inclusion of zero catches would introduce another variable, namely the complete absence of larvae, as opposed to merely not catching them. Where more than one net was used at a station, all samples, including zero catches, were considered when any net caught a tuna larva. Histograms showing the average catch per thousand cubic meters of water strained are presented in figure 3.

Of the several tendencies apparent in figure 3 perhaps the most noteworthy is the over-all decline in catch with depth. About 75–80 percent of the larvae occurred between the surface and 60 m., about 20–25 percent between 70 and 130 m., and practically none below this depth (closing nets operating from 332–127 m., and from 812–355 m. failed to capture tuna larvae on *Hugh M. Smith* cruise 33). In the night hauls a marked decrease was evident between the surface, 0–60, 70–130, and 140–200 m. captures, with the catches of the 0–200 m. tows being midway in number between those from the surface and 140–200 m. In the day hauls, on the other hand, there was a slight increase in catch with depth between the

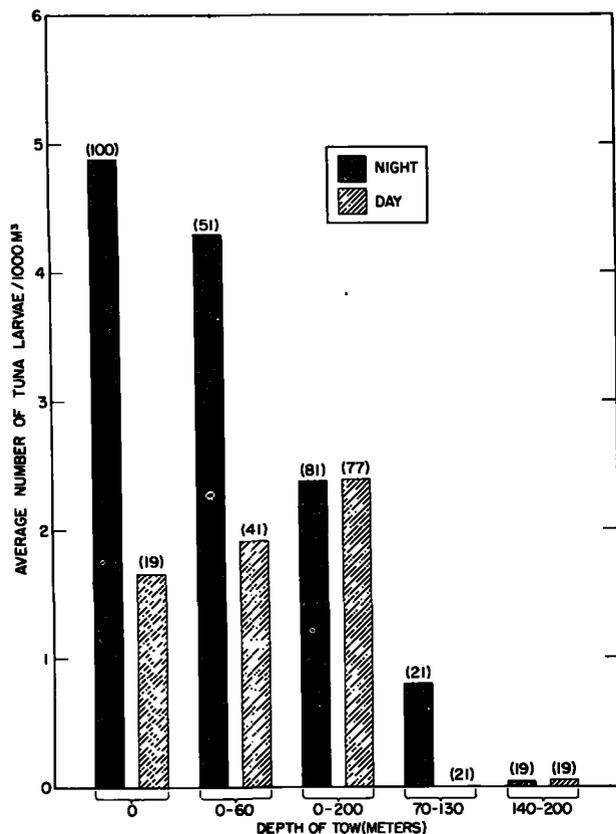


FIGURE 3.—Night and day variation in larval tuna catch with depth. Number of tows is shown in parentheses. The number of larvae obtained at each depth were as follows: 0 m.—927; 0-60 m.—432; 0-200 m.—592; 70-130 m.—20; and 140-200 m., 2.

surface, 0-60, and 0-200 m. tows. This illustrates an additional point as follows: the increase with depth may indicate a reduction in the amount of dodging with a decrease in illumination, or it may represent a downward migration during the daylight hours. This contrasts with the situation found for night catches where the density of larvae was much greater toward the surface. Such a change in abundance obviously signifies vertical migration, and, although dodging is a factor, we believe that migration is of greater importance in determining the number of larvae captured at a given depth and time.

Another tendency shown in figure 3 is the night-day difference in catch at various depths. This difference is most marked in the surface tows, less between 0 and 60 m., of dubious status at 70-130 m. because of the small numbers involved, and apparently lacking at 140-200 m. The average

catch of the 0-200 m. tows (which encompassed this entire range) showed no night-day difference. The fact that the night-day ratio decreased with depth cannot be used to evaluate the separate effects of vertical migration and net-dodging, and it is of interest here chiefly because of its bearing on sampling vagaries. Shallow tows (0 or 0-60 m.) caught about half as many tuna larvae during the day as at night, whereas 0-200 m. tows caught the same number during each period. Deep closing-net tows (70-130 and 140-200 m.) showed little or no night-day differences, but their catches were too small for good comparisons.

In comparing the catches made at different towing depths the question arises as to whether larval tuna are at times restricted to the upper layers by temperature. Some evidence that they are restricted in this manner is given in figure 4, where the temperatures at various depths are plotted against closing net catches from these depths (sampling was completely stratified in time and space). Here the larvae can be seen to abound in the warm surface layers, and all captures at 70-130 m. were made where the water was 60°F. or warmer. One of the two larvae taken at 140-200 m. was captured at a station where a tongue of 60°F. water projected well down into this depth range, but no explanation

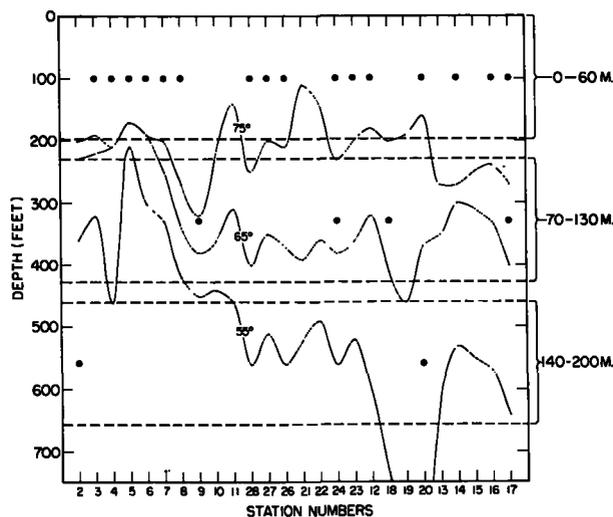


FIGURE 4.—Isotherm depths at plankton stations, *Hugh M. Smith* cruise 33. Stations are ranked from north to south; temperature and depth measurements derived from bathythermograph traces. Dots represent closing net tows yielding tuna larvae.

is offered for the larva taken in 52–55°F. water between 140 and 200 m. Aside from this one instance, it appears that 60°F. is the minimum temperature at which tuna larvae occur.

TABLE 2.—Correlation between larval tuna catches made by 0 meter, 0–60 m., and 0–200 m. tows on Hugh M. Smith cruise 38

[Analyses performed on data transformed by r'
= $\log \left(\frac{r+1}{10,000 \text{ m}^3 \text{ of water strained}} \right)$]

Comparison between—	Number of stations considered	Calculated r -value
First 0 m. and 0–200 meters.....	12	–0.03
Second 0 m. and 0–200 meters.....	13	0.10
First 0 m. and 0–60 meters.....	14	*0.67
Second 0 m. and 0–60 meters.....	14	*0.60
0–60 meters and 0–200 meters.....	14	0.22

*Indicates a significant r -value ($p < 0.05$).

**Indicates a highly significant r -value ($p < 0.01$).

The above data on vertical distribution and night-day variations are of aid in selecting sampling times and depths, but the basic reason for sampling larval tuna is to obtain estimates of their abundance. In order for these estimates to be meaningful it is requisite that they reflect the presence of all tuna larvae, or, in other words, one should be able to say that there are x larvae beneath y areal units of sea surface. If a plankton tow samples all of the larvae beneath a given surface area then its catch provides an estimate of absolute abundance. If the tow captures a fixed percentage of the larvae, then an abundance estimate can be made providing a conversion factor is available. Obviously a tow which catches no set portion of the larvae is useless in furnishing a reliable abundance estimate. With these points in mind it is well to consider the utility of the information afforded by the various plankton tows discussed above.

It has already been shown that larval tuna occur from the surface to depths of 140 to 200 m. Of the several tows considered, the 0–200 m. is the only one sampling this entire distribution, so that its catch is the best reference for comparative purposes. On cruise 38 of the *Hugh M. Smith*, 0–60 and 0–200 m. tows were taken simultaneously (from the same towing cable) each night, and these were followed by two successive one-half hour surface tows. Although these tows differed slightly from each other with respect to time and space they are the best available for the comparison, and correlation methods were used to deter-

mine the proportionality of their catches. The correlation analyses are summarized in table 2, where all species of tuna larvae were pooled and stations were disregarded if neither net captured a larval tuna. As in the analysis of reliability, the data were heteroscedastic, and a transformation in the form $x' = \log \left(\frac{x+1}{10,000 \text{ m}^3 \text{ water strained}} \right)$ was necessary.

The data in table 2 show that neither the surface nor the 0–60 m. tow captured a fixed fraction of the 0–200 m. catch. There were significant correlations between the surface and 0–60 m. captures, but these are of little importance because neither net sampled the entire vertical distribution of the fish. In the 0–60 m. and 0–200 m. tows, at least, the deep net sampled depths fished more extensively by the shallower net, and one would accordingly expect a “part-whole” correlation between their catches.

Figure 5 shows the tracks and catches of 0–60 and 0–200 m. tows at two stations where these nets were used simultaneously; at one station the catches were equal, at the other they differed considerably. Fishing depths were calculated from observed wire-angles, and thermocline depths from bathythermograph records. The dashed intercept lines of figure 5 delimit the time intervals in which the 0–200 m. tow fished in the

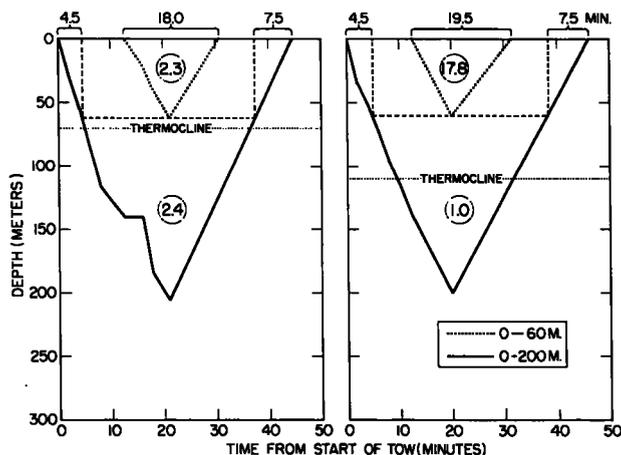


FIGURE 5.—Catch-depth-time relations for two stations where 0–60 m. and 0–200 m. tows were operated simultaneously at night (*Hugh M. Smith* cruise 38, stations 45 and 82). Left figure shows situation where catches were the same, right figure shows situation where catches were considerably different. Circled values represent catch (total tuna larvae per 1,000 cubic meters strained).

depth range of the 0-60 m. tow, these amounting to 12 minutes for each station. For the left panel of figure 5, the total 0-200 m. catch should be twelve-eighteenths of the 0-60 m. catch plus an additional catch, C_1 , taken at depths greater than those fished by the 0-60 m. net. For the right panel, the comparable expression would be $12/19.5 \times (0-60 \text{ m. catch}) + C_2$. Substituting the 0-60 m. catch values, these expressions reduce to $1.5 + C_1$ and $11.0 + C_2$ larvae/1000 cubic meters. The former is a reasonable approximation of the actual 0-200 m. catch of 2.4 larvae/1000 cubic meters, whereas the latter differs decidedly from the actual catch of 1.0 larvae. The majority of 12 other stations similarly analyzed also showed marked differences, suggesting that the disproportionality between the 0-60 m. and 0-200 m. catches may be caused by a spotty distribution of tuna larvae. Thermocline depth did not appear to be related to the catch, although there were indications of a catch decline when the 0-200 m. net fished deeper than the 60° isotherm.

In the preceding discussion the abundance of larval tuna was expressed in terms of the volume of water strained. The conversion of this measure to one based on areal units of sea surface was accomplished with the aid of the following conventions. It seemed obvious that only those tows fishing throughout the vertical range of tuna larvae could furnish accurate information on the number of larvae beneath a given surface area. Of the various tows studied, the 0-200 m. was the only one meeting this depth requirement, with a special situation existing for 3-level closing nets. Transformation of the 0-200 m. data involved multiplying the number of larvae per cubic meter strained by 200 (the depth of tow in meters) to give the number beneath 1 square meter of surface, and then multiplying this value by 10 to give the number beneath 10 square meters. (This area of sea surface was selected as a standard since it gave abundance estimates of about the same magnitude as the number of larvae captured per tow.) Multiplication by depth presupposed that sampling was equally intense at all depths, an assumption borne out by the relatively smooth tracks of the 0-200 m. nets shown in figure 5.

POFI's 3-level closing nets fished at depths of approximately 0-60, 70-130, and 140-200 m., so

that essentially the entire 0-200 m. depth range was sampled. The cumulative areal abundance estimate furnished by these 3 nets should nearly equal that of a 0-200 m. net if a similar conversion were made. In this case, however, the depth multiplier for each net was 60 (meters), and the "surface" occurred at 0, 70, and 140 m., respectively.

Figure 6 depicts the 0-60, 70-130, 140-200, and 0-200 m. data of figure 3 expressed as the number of larvae beneath 10 square meters of sea surface. It is apparent from figure 6 that the sum of the catches of the triple-net tows was less than the 0-200 m. catch, particularly during the day. Because of the two 10 m. gaps in the triple nets' depth range one might expect about a 10-percent differential (20/200) between the two catches. Because the inequality was 36 percent for the night hauls and 76 percent for the day hauls a

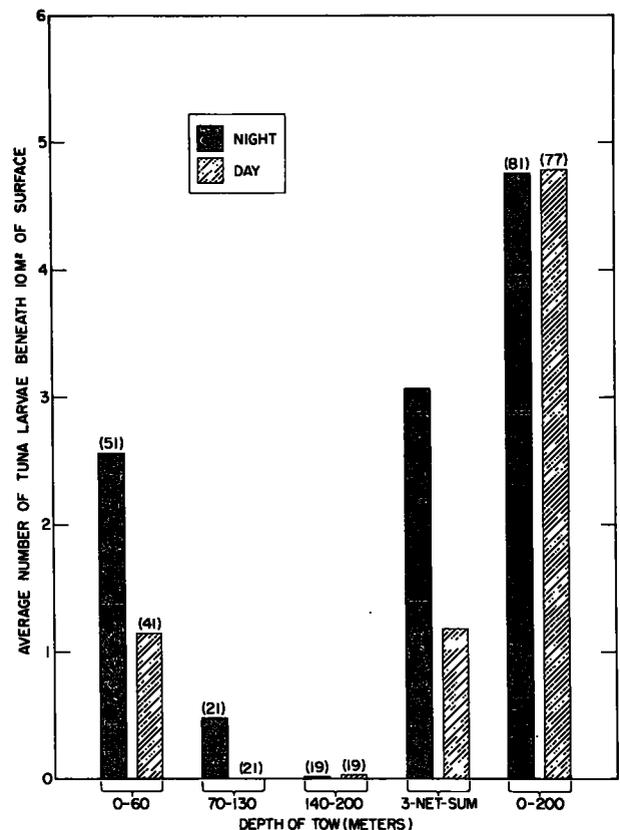


FIGURE 6.—Night-day variation in larval tuna catch with depth, expressed in terms of areal catch. Number of tows is shown in parentheses. The number of larvae obtained at each depth was as follows: 0-60 m.—432; 70-130 m.—20; 140-200 m.—2; and 0-200 m.—592.

poor sampling stratification is suggested. The same calculations made for the stations where 0-200 m. and triple-net tows were made together (*Hugh M. Smith* cruise 33, stations 18, 20, 26, and 28) produced a similar disparity (1.78 larvae/10m² for night 0-200 m. tows, and 0.91 larvae/10m² for night triple-net tows). How much of this is sampling artifact and how much is real can only be determined with more data.

It would appear that, of the various hauls employed, the 0-200 m. tow, by sampling the complete vertical range of larval tuna, produced the most useful information on their abundance. In addition, night-day catch variations were suppressed in this tow, although this might not be true in regions where a limiting isotherm, such as 60°, lies deeper than 200 m. Disadvantages of the 0-200 m. tow are that it may fish too deeply and its catch consists of relatively small numbers

of tuna larvae (large numbers are frequently needed for statistical or other reasons). In an attempt to obtain a more representative sample of larval tuna POFI is presently testing a 0-140 m. oblique open-net tow. It is believed that the 0-140 m. sampling range covers the vertical distribution of tuna larvae, that day-night variations in catch will be small or absent, and that the number of captures can be increased by taking two half-hour samples per station. Where the major sampling goal is the capture of large numbers of larvae, then shallow tows at night are a better choice. In table 3, which shows the frequency of occurrence of catches of different magnitude by the several types of tow, it is apparent that our largest catches were obtained at night in surface or 0-60 m. tows. The noticeable species differences in day-night catch are discussed in the following section.

TABLE 3.—Frequency of occurrence of catches of different magnitude in various types of tows

Species and where caught	When caught	Number of larvae/1000m ³ strained												
		0.1 to 3.9	4.0 to 7.9	8.0 to 11.9	12.0 to 15.9	16.0 to 19.9	20.0 to 29.9	30.0 to 39.9	40 to 59	60 to 99	100 to 199	500 to 1,000		
SKIPJACK														
Surface	Day	2	1											
	Night	40	9	6	3		1	2						
0-60 m.	Day	15	1											
	Night	22	7	2					1					
0-200 m.	Day	44	4			1								
	Night	45	6	1	1									
70-130 m.	Day													
	Night	5												
140-200 m.	Day													
	Night	1												
YELLOW FIN														
Surface	Day	5	1											
	Night	48	8	3	2		1	1						
0-60 m.	Day	19												
	Night	22	7	1	1		1							
0-200 m.	Day	34	2											
	Night	44	1											
70-130 m.	Day													
	Night	3												
140-200 m.	Day													
	Night													
FRIGATE MACKEREL														
Surface	Day													
	Night	17		1			1	1	2	2	3	1		
0-60 m.	Day	8												
	Night	6	3	1			2	2		1	1			
0-200 m.	Day	2												
	Night	4												
70-130 m.	Day													
	Night													
140-200 m.	Day	1												
	Night													

Diurnal Variation in Shallow-Tow Catches

Considering diurnal fluctuations in abundance, Wade (1951) found skipjack in 17 percent of his night surface samples but in only 3.6 percent of his day surface samples. He found a similar situation for what he termed *Euthynnus yaito*

(little tunny), which was in reality frigate mackerel (Matsumoto, personal communication), but not for yellowfin. For the latter species, day and night tows were equally successful in capturing larvae, and high catches occurred randomly throughout a 24-hour period. Matsumoto (1958)

noted a striking day and night disparity in the catch of "tuna larvae" (three species plus an unidentified category, combined) taken by surface tow, but any differences between skipjack and frigate mackerel, on the one hand, and yellowfin, on the other, were masked by his pooling of species. Actually his data (see below) included nearly 50 percent more skipjack and frigate mackerel, combined, than yellowfin.

The catch of tuna larvae at various times of day and at two sampling depths is shown in figure 7. Included are Matsumoto's data from *Hugh M. Smith* cruise 6, excluding his unidentified category. It is obvious that skipjack and frigate mackerel were infrequently captured at the surface during the day but were often taken there in numbers at night. Yellowfin were ir-

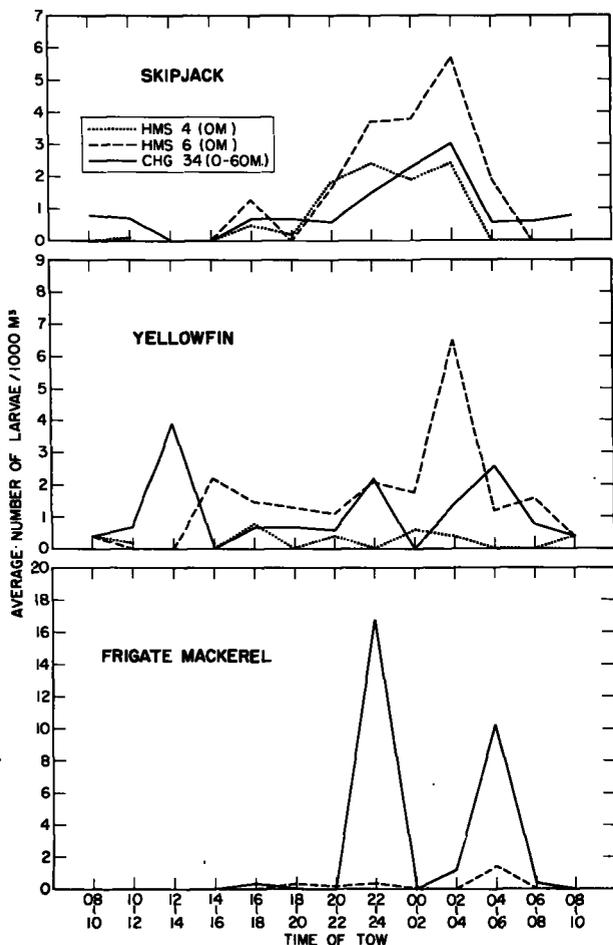


FIGURE 7.—Larval tuna catch by surface and 0-60 m. tows at various times of day. All data are from Hawaiian waters.

regularly distributed throughout a 24-hour period, with low surface catches occurring chiefly at mid-morning. Skipjack showed about the same diurnal distribution in the 0-60 m. catches as in the surface captures, whereas the 0-60 m. frigate mackerel captures were much greater than at the surface. The 0-60 m. yellowfin catch was irregularly distributed and showed no clear relation to the surface catch. This pattern of an increase in catch at night could be caused by either vertical migration or less successful dodging as discussed previously. If dodging only were involved one would expect the catch to be essentially constant during the hours of darkness. In the case of skipjack this is manifestly not so, for the catch increased markedly between 1800-2000 and 0200-0400 hours, during which time illumination remained the same. Vertical migration therefore appears to be the major factor causing the increase in surface catch at night.

Another point illustrated by figure 7 is that surface captures of yellowfin and skipjack commenced in the afternoon, with yellowfin appearing in the catch earlier than skipjack. During the period from 1800-2000 hours, however, both species were uncommon or lacking in the surface catches. This is the time of sunset, and it also marks the beginning of the ascent of the deep-scattering layer and of invertebrate plankton. Subsequent to sunset, the larvae of both tunas increased in the surface catches. In order to investigate the effects of sunset on larval tuna abundance, 6 half-hour surface tows were taken off Oahu just before and after sunset on each of two consecutive days. An EDO depth recorder was used to measure the depth of the various scattering layers, but good traces were obtained by this instrument on only one night. The larval tuna and invertebrate plankton catches made during the two nights, along with the EDO traces obtained on one night, are shown in figure 8. It should be pointed out that in the figure, the plotted times of capture for larval tuna and invertebrate plankton represent the midpoints of the half-hour towing intervals.

The larval tuna catches shown in figure 8 indicate a late afternoon increase in surface abundance for yellowfin but not for skipjack. The invertebrate plankton volumes peaked just after sunset, and declined thereafter. The two deep

scattering layer traces obtained became inseparable from each other and from the surface trace at about the time when plankton volumes were greatest and the larval tuna catch the least. It seems evident that the change in environmental conditions accompanying sunset had marked effect on the surface abundance of tuna larvae and invertebrate plankton, and on the position of the deep scattering layer. It is likely that these items are themselves interrelated.

Some contemporary thought holds that euphausiids and other crustacean plankters are the principal components of this layer (Boden 1950, Moore 1950). Our data showing an increase in surface plankton concurrent with the rise of the deep scattering layer are in accord with this idea, although copepods and other small crustacea were considerably more abundant than euphausiids in the samples under consideration. Supposedly these plankters are phototactic and migrate to maintain position at a weak state of illumination, with their movement to the surface at twilight being a response to fading light (Clarke and Backus, 1956). Although this explanation accounts for the twilight peaking in surface plankton it does not explain the marked decline occurring shortly after sunset. This decline is real, for it was found on two successive days in the present study and has been noted several times by E. L. Nakamura.¹

The question now arises whether tuna larvae are important constituents of the deep scattering layer. The following lines of evidence indicate that they are not: the surface abundance of larval tuna was complementary to that of the deep scattering layer of invertebrate plankton at sunset; larval skipjack and yellowfin were commonly taken at the surface during the afternoon, well before the deep scattering layer arrived at the surface; and our deep closing net samples indicated extremely scanty abundance of tuna larvae at 140–200 m., so that it is unlikely that they occur at the 350–550 meter depths occupied by the deep scattering layer prior to ascent.

Relation of Larval Tuna to Invertebrate Plankton

It was noted that larval tuna and invertebrate plankton were complementary in abundance at twilight, and it was deemed worthwhile to examine this relation further. A plot of the larval

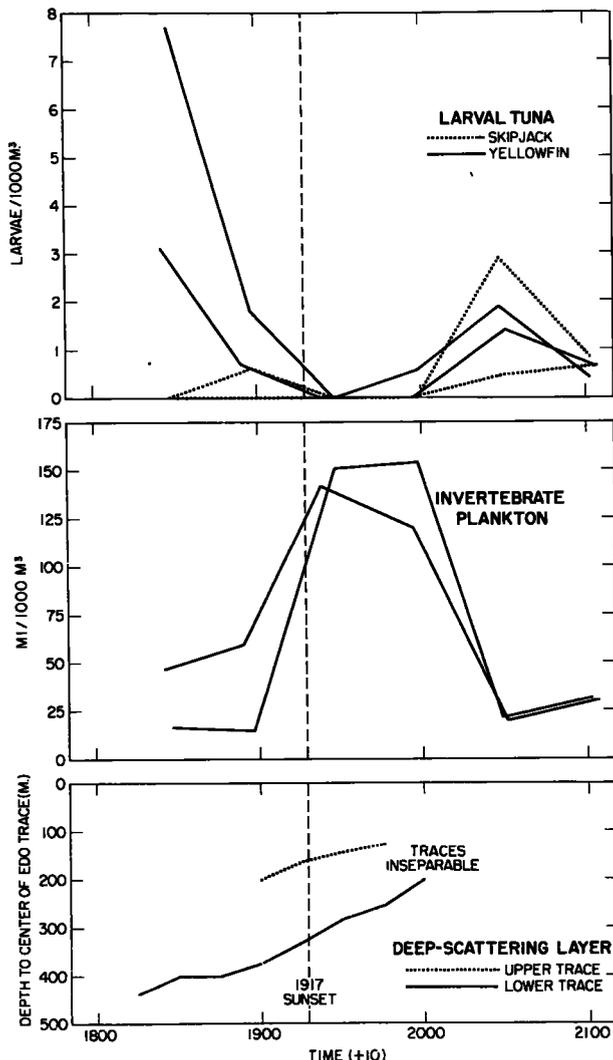


FIGURE 8.—Effect of sunset on larval tuna and invertebrate plankton catches, and depth of deep-scattering layer, as observed on *Charles H. Gilbert* cruise 34, stations 4 and 13, June 21–22, 1957. Plotted time for larval tuna and plankton catches is midpoint of towing interval.

tuna catch (skipjack and yellowfin combined) with the accompanying invertebrate plankton volumes is given in figure 9. The plankton data were obtained from the report of King and Hida (1954) (*Hugh M. Smith* cruises 4 and 6) and from unpublished information in the POFI files (*Hugh M. Smith* cruise 38 and *Charles H. Gilbert* cruises 30, 32, and 34). The dotted line in figure 9 was fitted by eye to enclose the maximal situations of abundance.

¹ Unpublished data in POFI files, Bureau of Commercial Fisheries Laboratory.

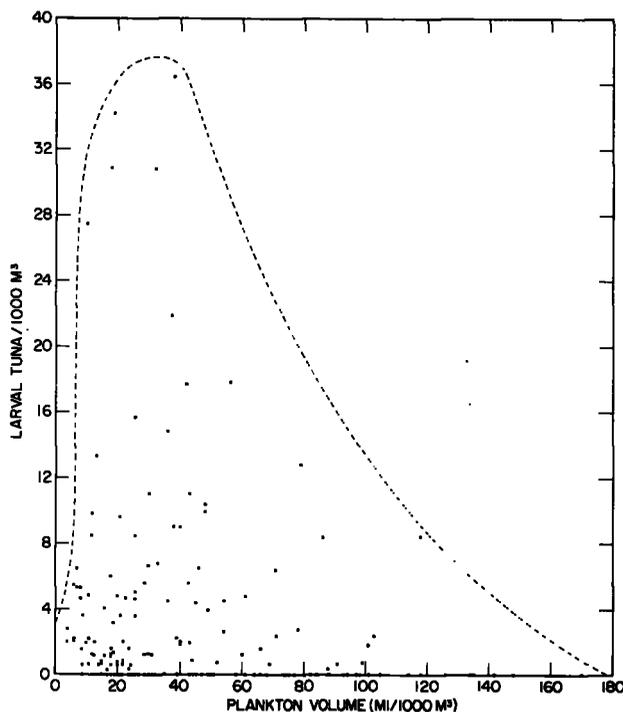


FIGURE 9.—Number of larval skipjack and yellowfin (combined) in relation to accompanying invertebrate plankton volumes. Data derived from 177 samples taken at 0 m. or 0-60 m. between evening and dawn. Curve fitted by eye to include maximal points.

In figure 9 it is seen that all of the large catches of tuna larvae were accompanied by small or moderate volumes of invertebrate plankton (roughly 10 to 60 ml./1000 cubic meters). The catches lowest in plankton contained few larvae, as did those richest in plankton. A similar but more marked situation obtained for frigate mackerel (not shown). It might be hypothesized that the low plankton concentrations were associated with either low-nutrient water or with enriched water so new to the euphotic zone that it had not been exploited biologically. In neither case would larval tuna be expected to abound. At the other extreme, large numbers of invertebrate plankters could represent both successful biological exploitation and a low level of grazing by higher forms. Many plankton feeders, such as small fish, squid, and crustaceans are of value to adult tuna as food (Reintjes and King, 1953; King and Ikehara, 1956), so that in their absence few adult tuna would be present, and logically there would be a paucity of tuna larvae (unless tuna spawn in areas of poor forage).

The shape and skewness of the dotted line (fig. 9) were evident in the data segregated by species and by cruise, and pooling was only done to emphasize the maximal (limiting?) situations. The nearly vertical ascent of the left limb stood in contrast to the gradual descent of the right. Whether the right-hand slope represents invertebrates grazing on larval tuna is not known, but there is some evidence that the left slope does not depict tuna larvae feeding on invertebrates. Clemens (1956) found that juvenile tunas rejected invertebrate plankters as food but avidly fed on softer-bodied larval fish, and the single larval tuna containing food, an 8 mm. skipjack, dissected by the writer had eaten a fish larva one-third its length.

The apparent incompatibility between larval tuna and invertebrate plankton reminds one of the exclusion hypothesis of Hardy (1935). In the present investigation, it would seem more likely that the two groups of animals are showing a differential response to some stimulus, such as light intensity, rather than actively avoiding each other.

Length Distribution of Larval Tuna by Depth and Time

Knowledge of the relative abundance of various size groups is of considerable importance in the problem of sampling larval tuna. It is desirable to know the minimum size which can be captured by a given mesh, and the maximum size which can be taken at a certain towing speed. From the standpoint of tuna biology, relative size abundance provides information on growth and mortality.

For this report, size was expressed in terms of length, and total length was selected from the several length measurements used for fish (p. 233). Length was measured with the aid of a binocular dissecting microscope fitted with an ocular micrometer. Measurements were made to the nearest micrometer unit (0.095 mm.), and then converted to millimeters and tenths of millimeters. Because of body distortion and frayed fins these measurements were sometimes overly precise, but this has been remedied by grouping the fish in 1-mm. length categories.

The percentage frequency of occurrence by 1-mm. length groups of skipjack and yellowfin is shown in figure 10 for specimens collected on Hugh M. Smith cruises 4, 6, 31, and 33, and

Charles H. Gilbert cruise 34. Larvae between 3.0 and 5.9 mm. dominated the catch of both species. Since tuna larvae are thought to measure between 2.4 and 3.0 mm. at hatching (Matsumoto 1958) one would expect the 2.0-2.9 mm. category to predominate, and the fact that it did not do so indicates either an erroneous impression of hatching size, a different habitat for this group, or, more likely, escapement through the net meshes. These factors may also apply to the 3.0-3.9 mm. group, for it was exceeded in number by the 4.0-4.9 mm. category in most instances. The nets employed in capturing these fish had aperture widths of 0.66 mm. (body) and 0.31 mm. (rear section and bag). Large larvae (> 5 mm.) comprised only a small portion of the catch, and although this stems in part from their being fewer in number, it also reflects their increased agility and net-dodging powers.

Although the surface, 0-60 and 70-130 m. tows yielded similar length frequency distributions for yellowfin they did not do so for skipjack. The 0-60 m. samples contained more large skipjack larvae than those from the surface, whereas the 70-130 m. collections had more small skipjack larvae than either shallow tow. In the case of the 70-130 m. data, however, the small sample size tends to discredit any conclusions drawn.

Because samples from deeper than 60 m. contained few tuna larvae of any kind, the discussion of the temporal aspects of length distribution is limited to the surface and the 0-60 m. catches. These were segregated into day and night hauls and replotted as figure 11. Except for the yellowfin surface data the day samples contained few fish, and the slight contrasts may not be real. In general terms there appeared to be little difference between the day and night length distributions of the surface catches, but in the 0-60 m. data the two species were more variable. Here there was a tendency for more large skipjack to be taken at night than during the day, whereas in yellowfin the reverse was true. If these phenomena are not sampling artifacts they may represent behavior having to do with differential vertical migration and net-dodging. Some evidence points to the existence of different migrational patterns between skipjack and yellowfin, for in figure 7 it was shown that yellowfin were more commonly caught at the surface during the day than skipjack. These captures could also

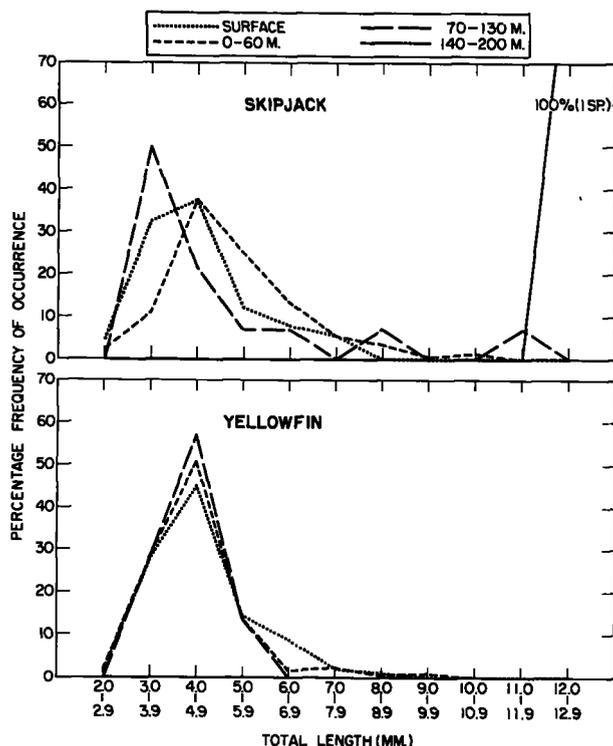


FIGURE 10.—Size variation of skipjack and yellowfin larvae in samples taken at various towing depths. Samples were collected at all times of day; percentages derived from the following catches: skipjack, 190 at 0 m.; 172 at 0-60 m.; 14 at 70-130 m.; and 1 at 140-200 m.; yellowfin, 311 at 0 m.; 183 at 0-60 m.; 7 at 70-130 m.; and 0 at 140-200 m.

have resulted from yellowfin being less adept at net-dodging, although this variable is difficult to assay.

Of the maximal sizes captured by surface tows, yellowfin were generally larger than skipjack (fig. 12); the difference in length between the yellowfin and skipjack larvae was fairly constant with various sampling times; and larger sizes of both species were taken with the advent of night. The last point indicates less successful dodging after dark, while the first two show that at a given time of day larger yellowfin than the skipjack can be captured, thus implying that yellowfin are slightly, but consistently, poorer dodgers. On the basis of casual observations of the adult swimming speeds, larval yellowfin may be slower swimmers than skipjack. The 0-60 m. data vary irregularly with sampling time but generally point out the diminishing effects of dodging as greater (darker) depths are sampled.

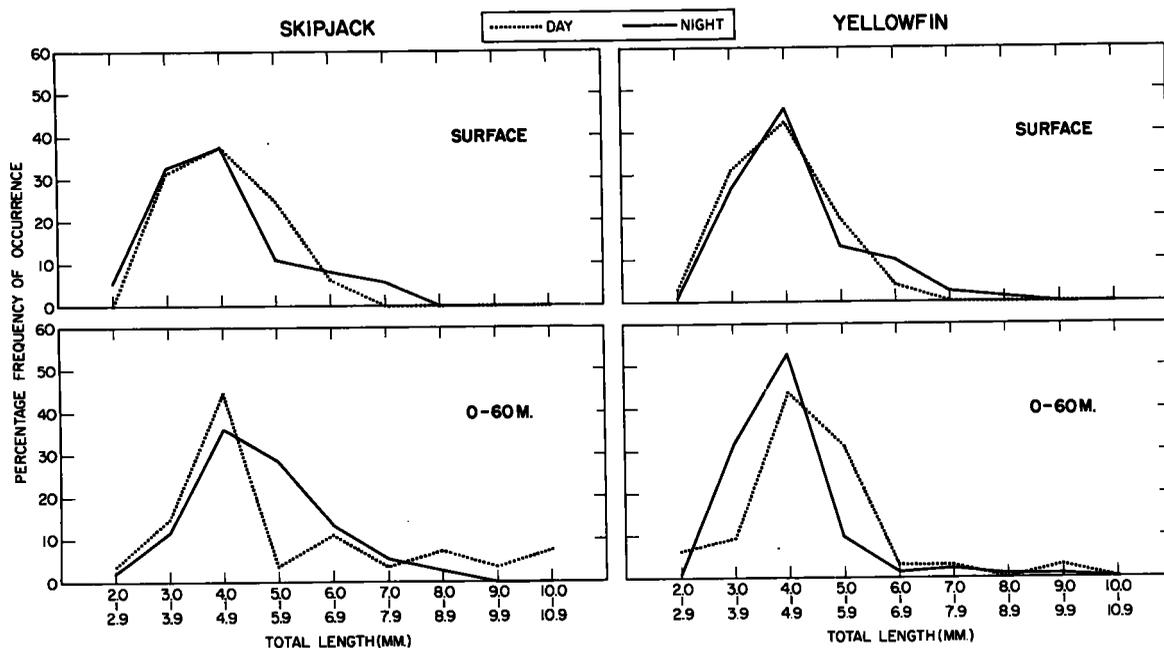


FIGURE 11.—Size variation of skipjack and yellowfin larvae in relation to time of sampling. Data derived from following catches: surface tows (skipjack) 16 day, 174 night; (yellowfin) 71 day, 239 night; 0-60 m. tows (skipjack) 27 day, 147 night; (yellowfin) 32 day, 144 night.

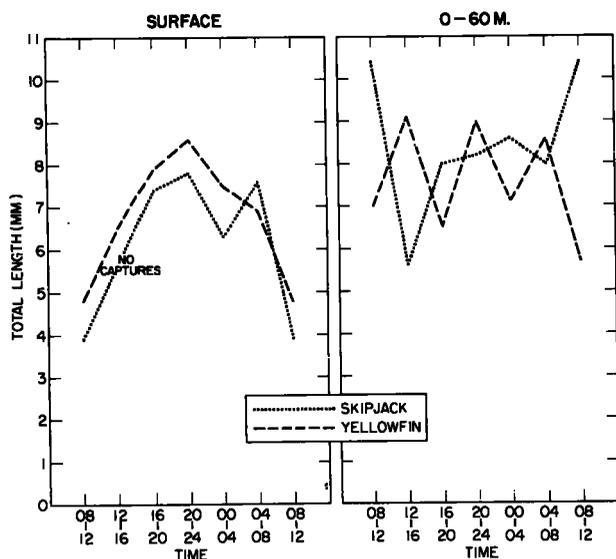


FIGURE 12.—Maximum length of tuna larvae captured at various times of day. Data derived from following catches: Surface tows, 190 skipjack and 311 yellowfin; 0-60 m. tows, 200 skipjack and 179 yellowfin.

ADULT VERSUS LARVAL TUNA ABUNDANCE

The determination of a numerical larval-adult tuna relation is of considerable practical value,

for if a definite numerical relation could be established it might result in the substitution of plankton nets for poles and longlines to provide estimates of abundance in exploratory fishing. An obvious limitation of this approach is that larvae contribute information only about the presence of spawning fish. In calculations of the larva/adult ratio particular attention must therefore be paid to the size of the adults caught, for it would be pointless to correlate the presence of larvae and immature adults.

It was shown earlier that of the various plankton tows employed, the 0-200 m. tow was the only one which sampled the entire vertical range of larval tuna. Where possible this sampling method has been used to provide estimates of larval abundance, with the catches being converted to the number of larvae beneath 10 square meters of sea surface, and the day and night samples being considered of equal reliability.

Yellowfin are sexually mature in appreciable numbers only at lengths greater than 120 cm. (Yuen and June, 1957); fish of this size are deep-swimming and best sampled by longlining (Murphy and Shomura, 1953). For yellowfin, therefore, only longline captures were considered, and

these were expressed as catch per hundred hooks. The data examined were taken from the reports of Murphy and Shomura (1953, 1955) dealing with the catches made on cruises 5, 7, 11, and 18 of the *Hugh M. Smith*. During these four cruises longline stations were accompanied by a 0-200 m. plankton tow on 55 occasions (see Matsumoto 1958). At 13 of these stations both larval and adult yellowfin were captured, at 25 stations only adults were taken, at 3 stations only larvae were captured, and at 14 stations neither larvae nor adults were taken. Only the 13 stations yielding both adults and larvae were analyzed, as it was reasoned that the absence of larvae might connote non-spawning (the absence of adults in the presence of larvae was infrequent and is not presently explicable). The data examined are presented in table 4. As previously shown, the larval data are skewed, and as pointed out by Murphy and Elliott (1954), so are those for adult yellowfin captured by longline. The data in table 4 were made approximately normal by transforming them logarithmically, and were analyzed by correlation methods which yielded a non-significant r -value of 0.422 ($r_{.05}=0.553$, Snedecor 1946: 149). It would appear from this, that for yellowfin either the larva/adult relation is not well defined, or that the individual catches are not reliable estimates of abundance.

TABLE 4.—Larval and adult yellowfin captured at the same station

<i>Hugh M. Smith</i> , cruise No.	Station	Larvae per 10 m ²	Adults per 100 hooks
5.....	2	1.5	3.2
7.....	16	0.9	2.3
7.....	24	1.3	3.4
11.....	4	2.9	1.2
11.....	6	1.4	0.8
11.....	8	5.2	9.5
11.....	9	4.1	5.0
11.....	10	5.7	15.7
11.....	11	8.2	10.3
11.....	12	2.1	7.9
11.....	22	4.6	29.3
11.....	23	1.5	13.0
18.....	4	3.2	0.4

Considerable difficulty was experienced in relating the abundance of larval and adult skipjack. The adults are essentially surface fish, so that it was necessary to derive abundance figures from the techniques peculiar to a live-bait fishery. This fishery provides two measures of abundance, one based on catch, the other on the number of schools sighted during scouting. Adult-larval

catch correlations could not be calculated because of a lack of plankton data, for in scouting, those observations attended by adequate plankton tows were generally secondary to other work programs. The available abundance estimates furnished by scouting thus suffer from inconsistency of effort and insufficient data on the number of fish comprising a school.

Despite these inadequacies there seemed to exist a rough relation between the numbers of larvae captured and schools seen, an example of which is shown in figure 13. The data used in this figure were derived from *Hugh M. Smith* cruises 33 and 38 (both primarily oceanographic) and *Charles H. Gilbert* cruise 32 (live-bait fishing). All three cruises investigated the waters of French Oceania and the central equatorial Pacific in January-March, the local skipjack season. For this study the region was divided into 13 areas (fig. 13) in accordance with the vessel tracks and certain oceanographic features. The number of hours of scouting and number of skipjack schools sighted were recorded by area, and from these figures a measure of abundance, expressed as the average number of skipjack schools sighted per 100 hours, was obtained. The data on adult abundance resulted from a total of 1,035 scouting hours in which 140 definitely identified skipjack schools were seen.

It would have been desirable to extract larval skipjack abundance figures from the captures made by 0-200 m. plankton tows, but unfortunately these tows were infrequent on the above cruises. As a consequence it was necessary to use the night catches of the 0 m. and 0-60 m. tows, both of which yielded about the same numbers of larval skipjack per station (see appendix tables 7, 8, and 10). As with the adult calculations, larval catch and effort were summarized by area, providing abundance estimates in terms of the average number of skipjack larvae per 1,000 cubic meters strained. The larval tuna data were based on a total of 406 skipjack larvae captured by straining 149,408 cubic meters of water.

The occurrence of larval skipjack coincided with that of adult schools, except for areas 6 and 11 (fig. 13). In addition, there was a general proportionality between the two variables, so that area 8 had large numbers of adults and larvae, the surrounding areas had small or moderate

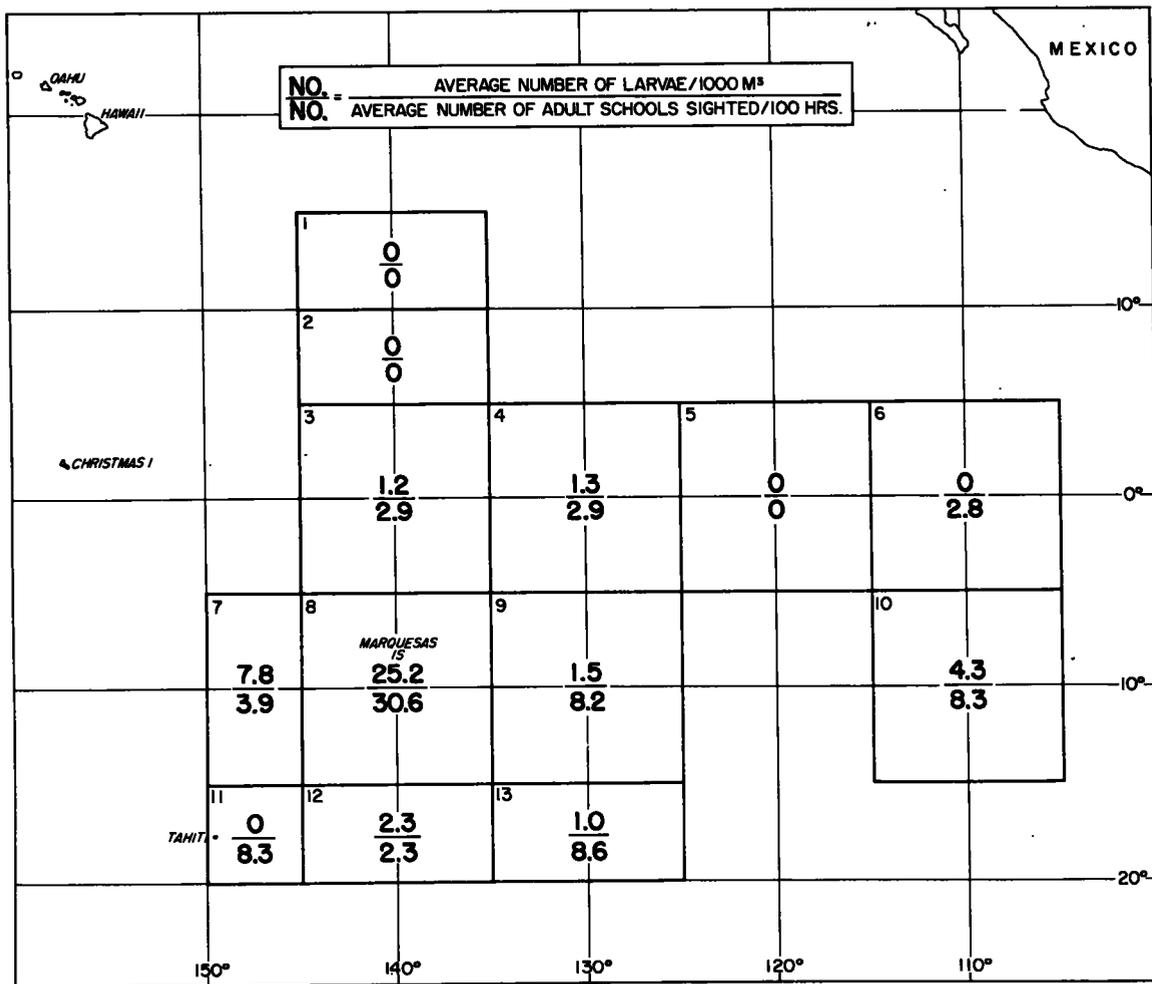


FIGURE 13.—Relation between numbers of larval and adult skipjack. Data from *Hugh M. Smith* cruises 33 and 38 and *Charles H. Gilbert* cruise 32. See text for details.

numbers of each, and the peripheral areas frequently lacked both. As with yellowfin, the data were transformed logarithmically and analyzed by correlation methods. Ignoring the zero records, a non-significant r -value of 0.611 was obtained ($r_{.05} = 0.754$, Snedecor 1946: 149). Again it could not be determined whether the lack of correlation resulted from a real lack of inter-relation or merely reflected the inadequacy of the estimates.

SUMMARY

(1) As a prelude to the collection and interpretation of data on larval tuna abundance, it was considered necessary to know the reliability of

the sampling methods, to standardize the time and depth of sampling for comparative purposes, and to understand certain facies of larval tuna behavior. This report deals with these problems by an analysis of the larval tuna catches made by 0, 0–60, 70–130, 140–200, and 0–200 m. plankton tows. These tows were taken during 15 POFI cruises in the waters of the Hawaiian Islands, the equatorial Pacific, and French Oceania.

(2) The use of paired plankton nets showed that the catch made by a single net could be duplicated and was therefore reliable within the limitations of the sampling method.

(3) Most tuna larvae were captured between the surface and 60 m. depth, with about 20–25 percent of the catch between 70 and 130 m., and

practically none between 140 and 200 m. There were marked night-day differences in catch at the surface but these became less as greater depths were sampled, and were not present in the 0-200 m. catches. Diurnal catch differences were attributed to migration to the surface at night and to dodging the nets during the day, with the former being of greater importance to the catch. Some evidence suggested that the 60°F. isotherm may be limiting to the occurrence of tuna larvae.

(4) When larval tuna catches were referred to areal units of sea surface it appeared that the 0-200 m. plankton tow, by sampling the complete vertical distribution of the fish, produced the most reliable abundance estimates. There was no apparent relation between the catch of this tow and of shallower tows made at the same time.

(5) Catch data from 0 and 0-60 m. tows showed that skipjack and frigate mackerel larvae were rarely captured during the day but were common at night. This tendency was less marked for yellowfin, particularly in the 0-60 m. tows.

(6) Both skipjack and yellowfin began to appear in the surface catch in the afternoon, but practically none were caught near sunset. Their temporary disappearance was correlated with the evening rise of the deep scattering layer and its associated invertebrate plankton. Further study showed an inverse relation between the numbers of larval tuna and invertebrate plankton volumes. Larval tuna did not appear to be constituents of the deep scattering layer.

(7) Measurements of larval tuna demonstrated that the dominant length group in the catch was from 4.0 to 4.9 mm. in total length. This size range predominated at each depth sampled, with slight non-modal shifts between day and night and between certain depths. Many larvae of the 2.0-2.9 mm. group may have passed through the net meshes, as may some of the 3.0-3.9 mm. category, and fish larger than 5 mm. were not common. Evidence derived from the larger larvae indicated that yellowfin were poorer dodgers than skipjack.

(8) No significant relation was found between the number of yellowfin taken by longline and the number of their larvae captured by 0-200 m. plankton tows. Similarly no significant relation was obtained between the number of skipjack schools sighted per 100 hours scouting and the number of larvae taken by 0 m. and 0-60 m. tows.

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APPENDIX

TABLE 5.—Larval tuna collected from surface hauls of one-hour duration on cruise 4 of the Hugh M. Smith in Hawaiian waters

[All data except for larval tuna are from King and Hida, 1954; only skipjack and yellowfin larvae considered]

Station No.	Position		Date	Time started	Water strained (m ³)	Number of fish in sample		
	North latitude	West longitude				Skipjack	Yellowfin	Total
1.	23°31'	161°07'	5/16/50	0934	2,255.3	0	1	1
1a	22°40'	161°15'	5/16/50	1722	2,604.7	6	7	13
2.	21°52.5'	161°07'	5/17/50	0240	2,504.5	0	0	0
3.	21°06'	161°05.5'	5/17/50	0925	2,699.9	0	2	2
4.	20°14.5'	161°07.5'	5/17/50	1640	2,124.9	0	0	0
5.	19°23.8'	161°06.3'	5/18/50	0028	2,231.5	2	0	2
6.	19°25'	159°50'	5/18/50	1048	2,271.9	0	0	0
7.	20°14.5'	159°50'	5/18/50	1835	2,967.4	0	0	0
8.	21°05'	159°50'	5/19/50	0255	2,472.3	5	4	9
9.	21°47.7'	159°51'	5/19/50	1000	2,585.2	1	1	2
10	22°40'	159°50'	5/19/50	1456	2,742.2	0	0	0
11	23°30'	159°50'	5/19/50	2316	2,704.2	12	0	12
12	22°40'	158°30'	5/19/50	0503	2,642.3	0	0	0
13	21°51'	158°29'	5/21/50	0150	2,906.2	16	0	16
14	20°58'	158°28'	5/21/50	1005	2,265.3	0	0	0
15	20°12.3'	158°30'	5/21/50	1610	2,950.2	0	0	0
16.	19°22'	158°28'	5/21/50	2253	3,017.4	2	0	2
17	18°32.5'	158°27.8'	5/22/50	0546	2,594.0	0	0	0
18.	18°32'	157°05'	5/22/50	1531	2,768.9	0	2	2
19.	18°24.3'	157°10'	5/23/50	0018	3,097.3	0	0	0
20.	20°14'	157°03.5'	5/23/50	0911	3,346.3	0	1	1
21.	20°58.7'	157°10.2'	5/23/50	1648	2,739.9	0	1	1
22.	21°53'	157°08.5'	5/24/50	0120	2,705.6	13	5	18
23.	22°40'	157°10'	5/14/50	1852	2,191.5	2	0	2
24.	22°45'	155°49'	5/14/50	0820	1,254.7	0	0	0
25.	21°54'	155°48.2'	5/24/50	1333	2,644.7	0	0	0
26.	21°02.5'	155°45.5'	5/24/50	2107	2,815.1	5	1	6
27.	20°30'	155°45'	5/25/50	0214	3,098.8	5	0	5
28.	18°33.5'	155°48'	5/25/50	1740	3,169.4	0	0	0

TABLE 6.—Larval tuna collected by 3-level closing nets on cruise 31 of the Hugh M. Smith (numerous samples not processed)

[All data, except larval counts, from King and others, 1957]

Station No.	Depth of tow (meters)	Position		Date 1955	Time started	Water strained (m ³)	Number of fish in sample				
		Latitude	Longitude				Skip-jack	Yellow-fin	Frigate mack-erel	Uniden-tified	Total
Test 1.	0-41'	20°38' N	157°49' W	9/23	1501(+10)	592.9	0	1	0	0	1
	59-89'					661.8	0	0	0	0	0
Test 2.	0-51'	17°46' N	157°09' W	9/24	1418	686.6	0	1	0	0	1
	56-110'					458.9	0	0	0	0	0
1.	0-92'	12°02' N	156°14' W	9/26	0939	814.1	0	0	0	0	0
	101-206					514.8	0	0	0	0	0
	226-403					562.1	0	0	0	0	0
3.	0-77'	10°42' N	156°04' W	9/26	2222	1,537.0	0	0	0	3	3
	52-137					1,083.0	0	0	0	0	0
4.	0-63'	09°24' N	155°50' W	9/27	1005	1,113.6	1	0	0	0	1
	61-127					921.5	0	0	0	0	0
	137-240					1,482.8	0	0	0	0	0
6.	0-74'	07°50' N	155°16' W	9/27	2309	1,480.7	2	4	0	0	6
7.	0-76'	06°42' N	154°54' W	9/28	0948	1,577.7	1	0	2	0	3
	68-160					933.7	0	0	0	0	0
	151-306					360.4	0	0	0	0	0
9.	0-74'	05°26' N	154°52' W	9/28	2215	1,681.7	1	0	0	0	1
	76-158					984.4	2	3	0	0	5
10.	72-133	05°26' N	154°22' W	9/29	0633	508.2	0	0	0	0	0
12.	0-60	06°30' N	153°18' W	9/29	2218	1,542.9	0	0	0	0	0
13.	0-63'	07°30' N	152°07' W	9/30	0928	1,298.4	5	0	0	0	5

¹ Data not reported by King et al. because of damage or malfunctioning of gear or other reasons. Most of these data not incorporated in present analysis.

TABLE 6.—Larval tuna collected by 3-level closing nets on cruise 31 of the Hugh M. Smith (numerous samples not processed)—Continued

[All data, except larval counts, from King and others, 1957]

Station No.	Depth of tow (meters)	Position		Date 1955	Time started	Water strained (m ³)	Number of fish in sample				
		Latitude	Longitude				Skip-jack	Yellow-fin	Frigate-mackerel	Unidentified	Total
15	66-132	08°26' N	150°54' W	9/30	2157	833.0	2	0	0	0	2
16	0-64	09°13' N	149°48' W	10/1	0932	1,285.6	0	0	0	0	0
	52-145					1,026.8	0	0	0	0	0
19	115-346	11°32' N	148°13' W	10/2	0845	1,008.5	0	0	0	0	0
21	0-59	10°55' N	147°10' W	10/2	2300	1,503.2	0	2	0	0	2
21	161-300					360.4	0	0	0	0	0
22	171-315	10°10' N	146°08' W	10/3	0929	851.8	0	0	0	0	0
24	0-68	09°40' N	144°54' W	10/3	2153	1,502.7	0	1	1	0	2
	141-259					1,197.1	0	0	0	0	0
25	0-75	09°02' N	143°57' W	10/4	0918	1,298.2	0	0	2	0	2
27	0-71	08°34' N	142°34' W	10/4	2201	1,502.2	0	2	0	1	3
	47-132					1,772.8	0	0	0	0	0
28	0-57	08°06' N	141°24' W	10/5	0923(+0)	1,500.9	0	4	0	0	4
	63-135					1,310.3	0	2	0	0	2
30	0-68	08°55' N	140°02' W	10/5	2155	1,349.1	3	0	0	2	7
	59-137					1,740.8	0	0	0	0	0
	131-259					1,408.7	0	0	0	0	0
33	80-129	10°20' N	137°43' W	10/6	2155		0	0	0	0	0
34	90-128	11°10' N	136°30' W	10/7	0931		0	0	0	0	0
	141-303					1,077.3	0	0	0	0	0
36	59-160	10°45' N	135°36' W	10/7	2152	1,355.7	0	0	0	0	0
37	0-79	10°10' N	134°12' W	10/8	0931	1,374.7	0	1	0	0	1
	61-152					1,019.6	0	0	0	0	0
42	66-143	09°31' N	129°53' W	10/9	2155	737.7	0	0	0	0	0
	147-279					1,195.7	0	0	0	0	0
43	80-170	10°03' N	128°18' W	10/10	0938	521.0	0	0	0	0	0
	180-334					760.5	0	0	0	0	0
45	54-167	10°30' N	127°18' W	10/10	2156(+8)	825.4	0	0	0	0	0
46	184-305	10°55' N	126°12' W	10/11	0937	404.4	0	0	0	0	0
48	0-60	11°36' N	125°00' W	10/11	2142	1,201.7	0	0	2	0	2
	61-143					545.2	0	0	0	0	0
49	0-68	12°11' N	123°48' W	10/12	0933	1,426.4	0	0	0	0	0
	66-141					882.6	0	0	0	0	0
	147-256					916.6	0	0	0	0	0
51	0-41	11°20' N	122°28' W	10/12	2137	1,432.6	0	0	6	0	6
	61-130					988.3	0	0	0	0	0
	137-276					882.2	0	0	0	0	0
52	0-59	10°19' N	121°13' W	10/13	0927	1,715.2	0	1	2	0	3
	137-300					648.2	0	0	0	0	0
54	0-61	09°26' N	119°58' W	10/13	2137	1,438.7	0	0	0	0	0
	66-152					972.5	0	0	0	0	0
55	61-140	08°38' N	118°53' W	10/14	0934	265.9	0	0	0	0	0
	137-259					934.4	0	0	0	0	0
57	137-267	06°14' N	117°28' W	10/14	2138	1,222.4	0	0	0	0	0
58	0-82	09°56' N	115°55' W	10/15	0930	1,547.1	0	0	1	0	1
	61-162					1,176.5	0	0	0	0	0
	137-302					717.4	0	0	0	0	0
60	0-43	10°40' N	114°34' W	10/15	2142	1,160.4	0	1	0	0	1
	161-263					581.7	0	0	0	0	0
61	0-43	11°30' N	113°30' W	10/16	0925	1,332.8	0	2	0	0	2
	68-121					959.8	0	0	0	0	0
	151-259					842.4	0	0	0	0	0
63	42-156	12°22' N	112°27' W	10/16	2138(+7)	1,293.9	0	0	0	0	0
	94-315					1,039.7	0	0	0	0	0
65	61-126	07°00' N	108°37' W	10/27	2151	1,039.2	0	0	0	0	0
68	0-48	04°34' N	109°24' W	10/28	2123	1,372.7	0	0	0	0	0
	161-245					943.5	0	0	0	0	0
69	0-43	03°10' N	110°12' W	10/29	1027	1,178.2	0	0	0	1	1
	74-126					967.6	0	0	0	0	0
	165-263					955.7	0	0	0	0	0
71	0-45	02°10' N	110°54' W	10/29	2320	1,347.6	0	0	0	4	4
74	76-135	00°14' S	112°20' W	10/30	2127	475.2	0	0	0	0	0
	171-277					586.4	0	0	0	0	0
75	0-48	01°23' S	112°46' W	10/31	0922(+8)	1,335.9	0	0	0	1	1
	54-122					413.6	0	0	0	0	0
83	0-47	07°42' S	114°52' W	11/2	2127	1,204.4	0	0	0	0	0
	66-120					92.8	0	0	0	0	0
85	157-276	07°56' S	120°04' W	11/4	0926	686.8	0	0	0	0	0
87	80-135	06°44' S	119°59' W	11/4	2144	554.5	0	0	0	0	0
88	66-124	05°16' S	120°04' W	11/5	1024	804.3	0	0	0	0	0
90	50-139	04°15' S	120°00' W	11/5	2138	1,198.9	0	0	0	0	0
	68-205					1,334.0	0	0	0	0	0
91	0-40	02°48' S	120°06' W	11/6	0925	1,410.1	0	0	0	0	0
	74-126					437.2	0	0	0	0	0
	165-269					720.7	0	0	0	0	0
93	145-204	01°35' S	119°59' W	11/6	2141	429.2	0	0	0	0	0
108	0-47	04°32' N	119°49' W	11/9	0920	1,055.2	1	0	0	0	1
	78-136					1,006.7	0	0	0	0	0
	175-284					205.9	0	0	0	0	0
110	0-47	05°49' N	120°00' W	11/9	2122	1,390.8	4	0	0	0	4
	76-136					833.7	0	0	0	0	0
	171-284					781.1	0	0	0	0	0
111	66-127	05°10' N	121°20' W	11/10	0920	715.7	0	0	0	0	0
	147-257					1,060.5	0	0	0	0	0

† Data not reported by King et al. because of damage or malfunctioning of gear or other reasons. Most of these data not incorporated in present analysis.

TABLE 6.—Larval tuna collected by 3-level closing nets on cruise 31 of the Hugh M. Smith (numerous samples not processed)—Continued

[All data, except larval counts, from King and others, 1957]

Station No.	Depth of tow (meters)	Position		Date 1955	Time started	Water strained (m ³)	Number of fish in sample				
		Latitude	Longitude				Skip-jack	Yellow-fin	Frigate mackerel	Unidentified	Total
113	0-46	04°05' N	122°31' W	11/10	2124	1,365.4	0	0	0	0	0
	54-118					1,105.2	0	0	0	0	
114	0-46	03°01' N	123°47' W	11/11	0919	1,785.6	0	2	0	1	3
	102-124					155.3	0	0	0	0	
119	141-284	00°22' N	127°08' W	11/12	2137	697.8	0	0	0	0	
123	0-41	02°04' S	130°48' W	11/14	0947(+9)	1,080.6	0	0	0	1	1
	165-262					894.1	0	0	0	0	
125	0-47	01°00' S	131°42' W	11/14	2130	1,552.6	0	0	0	1	1
	66-136					234.6	0	0	0	0	
	147-284					955.9	0	0	0	0	
126	0-48	00°10' N	133°10' W	11/15	0921	1,590.3	0	0	0	0	
	61-122					1,137.3	0	0	0	0	
	140-187					1,539.3	0	0	0	0	
134	0-54	05°36' N	139°12' W	11/17	2230	1,192.9	1	1	0	0	2
	40-134					905.4	0	0	0	0	
	89-269					494.2	0	0	0	0	
135	0-40	04°32' N	139°11' W	11/18	1010	1,357.3	0	1	0	0	1
	66-116					1,034.1	0	0	0	0	
	147-256					960.3	0	0	0	0	
137	0-40	03°27' N	139°11' W	11/18	2128	1,502.7	0	0	0	1	1
	161-240					480.6	0	0	0	0	
139	0-45	02°27' N	139°13' W	11/19	0908	1,696.3	0	1	0	4	5
	70-130					716.3	0	0	0	0	
	179-207					444.1	0	0	0	0	
142	0-49	01°14' N	139°27' W	11/19	2129	1,718.1	0	0	0	0	
	54-143					499.7	0	0	0	0	
144	61-122	00°16' N	140°12' W	11/20	1005	38.0	0	0	0	0	
147	0-42	01°05' S	140°00' W	11/20	2130	1,465.9	0	0	0	0	
149	0-46	02°43' S	139°46' W	11/21	0906	1,340.0	0	0	0	0	
	61-118					878.6	0	0	0	0	
	137-237					824.6	0	0	0	0	
152	141-271	04°03' S	139°42' W	11/21	2117	621.5	0	0	0	0	
153	0-43	05°31' S	139°54' W	11/22	1008	1,339.8	0	0	0	0	
	63-126					966.4	0	0	0	0	
	141-268					761.9	0	0	0	0	
155	147-248	06°33' S	139°26' W	11/22	2128	987.9	0	0	0	0	
155	0-53	00°35' N	157°47' W	12/8	2121(+10)	1,463.0	0	0	0	0	

¹ Data not reported by King et al. because of damage or malfunctioning of gear or other reasons. Most of these data not incorporated in present analysis.

TABLE 7.—Larval tuna collected on Hugh M. Smith cruise 33 in equatorial waters

Station No.	Approximate depth of tow (meters)	Position		Date 1956	Time started (+10)	Water strained (m ³)	Number of fish in sample				
		Latitude	Longitude				Skip-jack	Yellow-fin	Frigate mackerel	Unidentified	Total
2	0-60	11°54.9' N	140°02' W	3/9	1019	2,020	0	0	0	0	0
	70-130					924	0	0	0	0	
	140-200					1,303	0	0	1	0	
3	0-60	10°52' N	139°57' W	3/9	2127	2,598	0	0	7	0	7
	70-130					1,547	0	0	8	0	8
	140-200					1,700	0	0	4	0	4
	0					2,352	0	0	19	0	19
4	0-60	10°51' N	139°58' W	3/9	2246	2,352	0	0	4	0	4
	70-130	09°35' N	140°05' W	3/10	0908	1,512	0	0	0	0	0
	140-200					1,171	0	0	0	0	
	0					1,265	0	0	0	0	
5	0-60	08°36.5' N	140°09' W	3/10	2118	1,600	0	0	2	0	2
	70-130					1,295	0	0	0	0	
	140-200					1,333	0	0	0	0	
	0					1,895	0	1	3	0	4
6	0-60	07°22' N	140°01' W	3/11	0916	1,232	0	1	3	0	4
	70-130					302	0	0	0	0	
	140-200					1,407	0	1	4	0	5
7	0-60	06°28.5' N	139°56' W	3/11	2113	1,206	0	0	0	0	0
	70-130					1,974	0	0	6	0	6
	0					2,225	0	1	0	0	1
8	0-60	05°10' N	139°51' W	3/12	0917	1,283	0	0	0	0	0
	70-130					1,890	0	0	0	0	
	140-200					1,247	0	0	0	0	
9	0-60	04°08' N	140°00' W	3/12	2200	2,342	0	0	0	0	0
	70-130					1,627	0	4	0	0	4
	140-200					202	0	0	0	0	

See footnotes at end of table.

TABLE 7.—Larval tuna collected on Hugh M. Smith cruise 33 in equatorial waters—Continued

Station No.	Approximate depth of tow (meters)	Position		Date 1956	Time started (+10)	Water strained (m ³)	Number of fish in sample				
		Latitude	Longitude				Skip-jack	Yellow-fin	Frigate-mackerel	Unidentified	Total
10	0-60	02°45' N	140°07' W	3/13	0934	1,588	0	0	0	0	0
	70-130					945	0	0	0	0	0
	140-200					1,442	0	0	0	0	0
11	0-60	01°48' N	140°13' W	3/13	2117	1,316	0	0	0	0	
	70-130					1,155	0	0	0	0	
	140-200					1,354	0	0	0	0	
12	0-60	00°29' N	140°06' W	3/14	0928	2,228	0	0	0	0	
	70-130					1,953	0	0	0	0	
	140-200					1,775	5	0	0	0	
13	0-60	00°40' S	140°07' W	3/14	2115	103	0	0	0	0	
	70-130					2,639	0	0	0	0	
	140-200					1,435	0	0	0	0	
14	0-60	01°58' S	139°46' W	3/15	0924	811	0	0	0	0	
	70-130					2,175	0	0	0	0	
	140-200					2,356	0	0	1	0	
15	0-60	03°00' S	139°54' W	3/15	2112	1,361	0	3	0	0	
	70-130					1,540	0	0	0	0	
	140-200					2,632	0	0	0	0	
16	0-60	04°03' S	140°07' W	3/16	0848	1,786	0	0	0	0	
	70-130					1,062	0	0	0	0	
	140-200					8	0	0	0	0	
17	0-60	05°03' S	140°16' W	3/16	1949	2,394	0	2	0	0	
	70-130					1,848	1	4	0	0	
	140-200					1,012	0	0	0	0	
18	0-60	00°11' N	139°53' W	3/18	2059	756	0	0	0	0	
	70-130					1,583	64	5	4	0	
	140-200					1,082	1	0	0	0	
19	0-60	00°06' N	139°37' W	3/19	1041	628	0	0	0	0	
	70-130					2,663	39	5	1	0	
	140-200					4,706	0	0	0	0	
20	0-60	00°00.6' N	139°25.4' W	3/19	2118	2,364	4	0	0	1	
	70-130					4,983	0	0	0	0	
	140-200					1,633	0	1	0	0	
21	0-60	01°07' N	140°07' W	3/20	2125	1,753	0	0	0	0	
	70-130					1,382	0	0	0	0	
	140-200					2,598	0	0	0	0	
22	0-60	01°06.4' N	140°08.8' W	3/21	0941	2,043	0	1	0	0	
	70-130					1,618	0	0	0	0	
	140-200					2,796	1	0	0	0	
23	0-60	01°05' N	140°09' W	3/21	1048	1,914	0	0	0	0	
	70-130					2,335	0	0	0	0	
	140-200					2,375	0	0	0	0	
24	0-60	01°06.2' N	140°10' W	3/22	2125	542	0	0	0	0	
	70-130					2,519	0	0	0	0	
	140-200					1,830	0	0	0	0	
25	0-60	01°05' N	140°09' W	3/22	0924	1,053	0	0	0	0	
	70-130					1,461	0	0	0	0	
	140-200					2,114	1	0	0	0	
26	0-60	01°06.2' N	140°10' W	3/22	2125	734	0	0	0	0	
	70-130					1,185	0	0	0	0	
	140-200					1,353	0	0	0	0	
27	0-60	01°09.2' N	140°30.4' W	3/23	2121	1,506	1	0	0	1	
	70-130					1,731	3	0	0	0	
	140-200					1,583	0	0	0	0	
28	0-60	01°11.7' N	140°32.9' W	3/24	1055	1,946	0	3	0	0	
	70-130					867	0	0	0	0	
	140-200					1,073	0	0	0	0	
29	0-60	01°13.9' N	140°35.4' W	3/24	2122	2,934	1	0	1	0	
	70-130					2,487	3	0	0	0	
	140-200					2,055	0	1	2	0	
30	0-60			3/24	2122	1,049	0	0	0	0	
	70-130					2,319	0	0	0	0	
	140-200					2,558	3	0	0	0	
31	0-60			3/24	2234	1,561	0	0	0	0	
	70-130					624	0	0	0	0	
	140-200					1,874	2	1	0	0	

¹ Nets came in open.² Estimated.

TABLE 8.—Larval tuna collected on Hugh M. Smith cruise 38 in equatorial waters and near French Oceania

Station No.	Approximate depth of tow (meters)	Position		Date 1957	Time started	Water strained (m ³)	Number of fish in sample					Total
		Latitude	Longitude				Skip-jack	Yellowfin	Frigate mackerel	Little tunny	Unidentified	
2.	0-200	00°02'N	124°56'W	1/22	2000(+8)	1,490	0	0	0	0	0	0
	0-60						619	0	0	0	0	0
	0	00°02'N	124°54'W		2042	1,939	0	0	0	0	0	0
5.	0-200	00°13'N	121°46'W	1/23	2000	2,110	0	0	0	0	0	0
	0-60						1,697	0	0	0	0	0
	0	00°12'N	121°44'W		2050	984	0	0	0	0	0	0
8.	0-200	00°13'N	118°49'W	1/24	2005(+7)	2,214	0	0	0	0	0	0
	0-60						1,925	0	0	0	0	0
	0	00°11'N	118°46'W		2050	913	0	0	0	0	0	0
11.	0-200	00°08'S	115°32'W	1/25	2000	2,101	0	0	0	0	0	0
	0-60						2,975	0	0	0	0	0
	0	00°06'S	115°30'W		2045	569	0	0	0	0	0	0
14.	0-200	00°01'S	112°14'W	1/26	2005	1,944	0	0	0	0	0	0
	0-60						2,707	0	0	0	0	0
	0	00°03'S	112°14'W		2050	615	0	0	0	0	0	0
16.	0-200	01°23'S	110°06'W	1/27	2000	1,772	0	0	0	0	0	0
	0-60						2,116	0	0	0	0	0
	0	01°23'S	110°04'W		2040	1,896	0	0	0	0	0	0
19.	0-200	04°43'S	109°45'W	1/28	2015	1,680	0	0	0	0	0	0
	0-60						2,110	0	0	0	0	0
	0	04°45'S	109°44'W		2055	1,702	0	0	0	0	0	0
23.	0-200	07°53'S	110°04'W	1/29	2005	849	0	0	0	0	0	0
	0-60						1,578	0	0	0	0	0
	0	07°55'S	110°02'W		2055	2,370	3	0	0	0	0	3
45.	0-200	02°58'S	129°55'W	2/25	2000(+9)	621	2	1	0	0	0	3
	0-60						1,535	3	0	0	1	5
	0	03°00'S	129°52'W		2122	1,449	13	0	0	0	5	18
47.	0-200	06°32'S	130°04'W	2/26	2100	2,465	2	3	0	1	0	6
	0-60						860	2	0	0	0	2
	0	06°30'S	130°01'W		2100	1,814	1	0	0	0	1	2
49.	0-200	10°00'S	130°00'W	2/27	2128	1,723	0	0	0	0	0	0
	0-60						2,277	3	1	0	0	4
	0	06°33'S	130°01'W		2210	781	0	2	0	0	0	2
51.	0-200	13°27'S	130°01'W	2/28	2115	1,750	10	1	0	0	0	11
	0-60						2,235	4	0	0	0	4
	0	10°00'S	129°58'W		2200	1,601	0	0	0	0	0	0
54.	0-200	13°30'S	130°00'W	2/28	2225	1,592	1	1	0	0	0	2
	0-60						2,726	0	0	0	0	0
	0	13°27'S	130°01'W		2130	925	1	1	0	0	0	2
57.	0-200	16°35'S	130°04'W	3/1	2215	1,815	0	0	0	0	0	0
	0-60						1,794	0	0	0	0	0
	0	16°30'S	130°04'W		2000	2,825	3	1	0	0	0	4
59.	0-200	18°03'S	131°53'W	3/2	2050	884	0	0	0	0	0	0
	0-60						1,473	0	4	0	0	4
	0	18°01'S	131°54'W		2115	1,481	0	1	0	0	0	1
64.	0-200	17°50'S	135°06'W	3/3	2040	2,026	0	1	0	0	0	1
	0-60						645	0	2	0	0	2
	0	17°55'S	140°25'W		2120	1,511	0	7	0	0	0	7
66.	0-200	17°55'S	142°28'W	3/5	2145	1,521	0	47	0	0	0	47
	0-60						1,404	0	1	0	0	1
	0	17°48'S	135°06'W		2000	482	3	0	0	0	1	4
75.	0-200	17°56'S	140°28'W	3/5	2035	1,180	8	5	0	0	0	13
	0-60						2,100	6	15	0	0	21
	0	17°55'S	140°25'W		2030	1,967	1	1	0	0	0	2
79.	0-200	17°55'S	142°28'W	3/6	2115	625	3	3	0	0	0	6
	0-60						1,391	0	2	0	0	2
	0	17°56'S	142°35'W		2139	1,391	0	1	0	0	0	1
82.	0-200	18°03'S	145°30'W	3/7	2030(+10)	2,061	0	1	0	0	0	1
	0-60						1,022	0	2	0	0	2
	0	18°02'S	145°31'W		2115	1,570	0	3	0	0	0	3
85.	0-200	18°02'S	145°30'W	3/7	2140	1,622	1	0	0	0	0	1
	0-60						2,184	0	0	0	0	0
	0	18°03'S	145°30'W		2000	968	0	0	0	0	0	0
88.	0-200	11°18'S	145°02'W	3/15	2040	1,682	0	0	0	0	0	0
	0-60						2,105	0	0	0	0	0
	0	11°18'S	144°59'W		2105	1,705	0	0	0	0	0	0
92.	0-200	08°12'S	145°12'W	3/16	2020	1,930	3	1	0	0	0	4
	0-60						557	0	1	0	0	1
	0	08°09'S	145°12'W		2105	1,515	0	2	0	0	0	2
95.	0-200	05°00'S	145°00'W	3/17	2130	1,209	0	2	0	0	0	2
	0-60						2,478	2	1	0	0	3
	0	05°01'S	144°57'W		2020	955	4	4	0	0	0	8
98.	0-200	02°04'S	144°56'W	3/18	2103	1,642	14	2	0	0	0	16
	0-60						1,506	3	0	0	1	4
	0	02°06'S	144°54'W		2100	2,932	2	1	0	0	0	3
101.	0-200	02°04'S	144°56'W	3/18	2100	1,010	10	8	0	0	0	18
	0-60						1,785	54	1	1	0	56
	0	02°06'S	144°54'W		2112	1,678	60	1	0	0	0	61
104.	0-200	02°04'S	144°56'W	3/18	2020	2,327	3	2	0	0	0	5
	0-60						936	10	2	0	0	12
	0	02°06'S	144°54'W		2108	1,445	7	1	2	0	0	10
107.	0-200	02°06'S	144°54'W	3/18	2134	1,451	9	4	0	0	0	13
	0-60											
	0	02°06'S	144°54'W		2134	1,451	9	4	0	0	0	13

TABLE 9.—Larval tuna collected on Charles H. Gilbert cruise 30 in French Oceania

[All tows were at the surface and of a half-hour's duration]

Station No.	Position		Date 1956	Time started (+9)	Water strained (m ³)	Number of fish in sample					Total
	Latitude	Longitude				Skip-jack	Yellow-fin	Frigate mackerel	Little tunny	Un-identified	
1	01°24.5'N	133°49'W	8/16	0959	1,804	0	0	0	0	0	0
2	00°24.5'N	133°09'W	8/17	0750	1,774	0	1	0	0	0	1
3	00°01'S	133°02'W		2000	1,570	0	1	0	0	0	1
				2041	1,597	0	0	3	0	0	3
					1,571	0	0	1	1	0	2
					1,533	0	0	1	0	0	1
4	00°54'S	132°22'W	8/18	0752	1,872	0	0	0	0	0	0
5	01°20'S	132°03'W		2003	1,572	0	0	0	0	0	0
				2039	1,309	0	0	0	0	0	0
					1,548	0	0	0	0	0	0
					1,555	0	0	0	0	0	0
6	02°44'S	131°42'W	8/19	0744	1,541	0	0	0	0	0	1
7	03°08'S	131°35'W		1959	1,562	0	0	0	0	1	1
					1,688	0	0	0	0	1	1
					1,373	0	0	0	0	2	2
					1,320	0	0	0	0	0	0
8	04°25.5'S	131°39'W	8/20	0746	1,670	0	0	0	0	0	0
9	04°49'S	131°48.5'W		2000	1,567	0	0	0	0	0	0
				2038	1,548	0	0	1	0	0	1
					1,610	0	0	0	0	0	0
					1,597	0	0	0	0	0	0
10	06°01.5'S	132°17'W	8/21	0746	1,678	0	0	0	0	0	0
11	06°19.5'S	132°10'W		1958	1,409	0	0	0	0	0	0
					1,392	0	0	0	0	0	0
					1,410	0	0	0	0	0	0
					1,413	0	0	0	0	0	0
12	07°32'S	132°05'W	8/22	0754	1,452	0	0	0	0	0	0
13	08°01.5'S	132°03'W		1957	1,775	1	0	0	0	0	1
					1,732	0	2	0	0	0	2
					2,035	2	0	0	0	0	2
					1,552	1	0	0	0	0	1
14	09°22'S	132°09.5'W	8/23	0747	1,670	0	0	0	0	0	0
15	09°48'S	132°07'W		1954	1,672	0	1	0	0	0	1
					1,649	0	0	0	0	0	0
					1,271	0	0	0	0	0	0
					1,249	0	0	0	0	0	0
16	10°51'S	132°00'W	8/24	0740	1,741	0	0	0	0	0	0
17	11°10'S	131°56'W		1957	1,705	0	0	0	0	0	0
					1,627	0	0	0	0	0	0
					2,035	1	0	0	0	0	1
					1,726	0	0	0	0	0	0
18	12°12.5'S	132°05'W	8/25	0750	1,891	0	0	0	0	0	0
19	12°31'S	132°04'W		1956	1,843	2	0	2	0	4	4
				2033	1,755	0	0	0	0	0	0
						1	0	0	0	0	1
20	13°30'S	132°15.5'W	8/26	0749	1,697	0	0	0	0	0	0
21	13°02.5'S	132°31'W		2002	1,540	17	0	0	0	0	17
					1,533	13	0	0	0	1	14
					1,687	25	0	0	0	1	26
					1,634	11	0	0	0	2	13
22	12°18'S	133°18'W	8/27	0749	1,418	0	0	0	0	1	1
23	12°02.5'S	133°33.5'W		2001	1,677	2	0	0	0	0	2
					1,561	2	0	0	0	2	4
					2,040	1	0	0	0	0	1
					1,587	1	0	0	0	0	1
24	11°33'S	134°33'W	8/28	0742	1,706	0	0	0	0	0	0
25	11°09.5'S	134°45.5'W		2002	1,737	1	1	0	0	0	2
					1,646	0	0	0	0	0	0
					1,545	0	0	0	0	0	0
					1,450	0	0	0	0	0	0
26	10°35'S	135°38.5'W	8/29	0800	1,706	0	0	0	0	0	0
27	10°17'S	135°52'W		1955	1,151	0	0	0	0	0	0
					1,107	0	0	0	0	0	0
					2,033	1	0	0	0	0	1
					1,322	0	0	0	0	0	0
					1,474	0	0	0	0	0	0
28	09°36.5'S	136°46'W	8/30	0801	1,562	0	0	0	0	0	0
29	09°21.5'S	137°01'W		2000	1,505	0	0	0	0	0	0
					1,482	0	0	0	0	0	0
					2,038	0	0	0	0	0	0
					1,216	0	0	0	0	0	0
30	08°43'S	137°52'W	8/31	0802	1,747	0	0	0	0	0	0
31	07°32'S	138°54'W	9/1	0756	2,021	0	0	0	0	0	0
32	07°39'S	138°56'W		1957	1,682	1	0	0	0	0	1
					1,806	4	0	0	0	1	5
					1,826	4	0	0	0	0	4
					1,521	2	0	0	0	0	2
33	08°50'S	139°08'W	9/2	0750	1,380	0	0	0	0	1	1
34	09°12'S	139°12'W		2005	1,457	1	0	0	0	0	1
					1,450	0	0	0	0	0	0
35	10°28'S	139°38'W	9/3	0754	1,188	0	0	0	0	0	0
36	10°00'S	139°41'W		1959	1,325	0	0	0	0	0	0
				2034	1,281	0	0	0	0	0	0

TABLE 10.—Larval tuna collected on Charles H. Gilbert cruise 32 in French Oceania; all tows were at the surface and of a half-hour's duration

Station No.	Position		Date 1957	Time started (+10)	Water strained (m ³)	Number of fish in sample					
	Latitude	Longitude				Skip-jack	Yellowfin	Frigate mackerel	Little tunny	Unidentified	Total
53	14°57' S	146°20' W	2/19	1937	1,490	36	15	0	2	0	53
54	14°17.5' S	145°31.5' W	2/20	0347	1,881	11	5	0	0	2	18
55	12°48.5' S	143°55' W	2/20	1941	1,834	0	1	0	0	0	1
56	12°05' S	143°06.5' W	2/21	0346	1,738	5	1	0	0	0	6
57	10°39' S	141°33' W	2/21	1933	1,760	4	4	0	0	0	8
58	09°55.5' S	141°03' W	2/22	0345	1,842	17	2	0	0	0	19
66	09°22.5' S	139°37' W	2/27	1936	1,467	6	0	0	0	0	6
71	08°57' S	139°54' W	3/2	2121	1,068	1	8	2	0	0	11

TABLE 11.—Larval tuna collected on Charles H. Gilbert cruise 34 in Hawaiian waters

[All tows were of a half-hour's duration]

Station No.	Approximate depth of tow (meters)	Position		Date 1957	Time started (+10)	Water strained (m ³)	Number of fish in sample					
		North latitude	West longitude				Skip-jack	Yellowfin	Frigate mackerel	Little tunny	Unidentified	Total
1	0-60	21°10'	158°19'	6/21	1240	1,538	0	6	0	0	0	6
3	0-60	21°09'	158°19'		1500	1,189	0	0	0	0	0	0
4	0-60	21°12.5'	158°21'		1742	1,644	2	4	0	0	0	6
	0	21°11.5'	158°20.5'		1813	1,282	0	4	0	0	0	4
	0	21°10.5'	158°20'		1840	1,377	0	1	0	0	0	1
	0	21°10'	158°19.5'		1909	1,504	0	0	0	0	0	0
	0	21°09'	158°19'		1942	2,061	0	0	0	0	0	0
	0	21°10.5'	158°20'		2015	2,156	1	3	0	0	0	4
	0	21°12'	158°20.5'		2049	1,540	1	1	0	0	0	2
6	0-60	21°11.5'	158°20'		2121	1,616	0	0	0	0	0	0
7	0-60	21°11'	158°19'	6/22	0013	1,742	1	0	0	0	0	1
8	0-60	21°11.5'	158°21'		0300	1,081	1	0	0	0	0	1
9	0-60	21°10'	158°19.5'		0622	1,933	2	0	0	0	0	2
11	0-60	21°10.8'	158°19.5'		0906	1,719	3	0	0	0	0	3
12	0-60	21°10'	158°18'		1154	1,371	1	1	0	0	0	2
13	0-60	21°12'	158°20.5'		1459	1,663	0	0	0	0	0	0
	0	21°11.5'	158°19'		1743	1,553	1	0	0	0	0	1
	0	21°11'	158°18.5'		1814	1,426	0	11	0	0	0	11
	0	21°11'	158°17.5'		1844	1,665	1	3	0	1	0	5
	0	21°10.5'	158°17'		1914	1,593	0	0	0	0	0	0
	0	21°10.5'	158°16'		1945	1,870	0	1	0	0	0	1
	0	21°11'	158°16.5'		2015	2,060	6	4	0	0	1	11
	0	21°11.3'	158°18.4'		2045	2,454	2	1	0	0	0	3
	0-60	21°11'	158°20.7'		2121	1,616	2	2	0	0	0	4
15	0-60	21°10.6'	158°19.5'	6/23	0001	1,724	7	0	0	0	0	7
16	0-60	21°11.3'	158°20.6'		0259	1,485	4	1	0	0	0	5
17	0-60	21°10'	158°20'		0603	1,543	0	0	0	0	0	0
18	0-60	21°10.5'	158°19.8'		0859	1,412	0	2	0	0	0	2
21	0-60	20°56'	157°50'		1652	1,253	1	0	0	0	0	1
22	0-60	21°10'	157°50'		1902	1,412	1	1	0	0	1	3
24	0-60	21°25'	157°21'		2305	1,354	4	0	41	1	0	46
26	0-60	21°37'	157°46.5'	6/24	0324	1,618	5	0	8	0	0	13
27	0-60	21°59'	157°45'		0621	1,570	1	4	2	0	0	7
28	0-60	22°20'	157°46'		0930	1,645	1	0	0	0	0	1
32	0-60	21°47'	158°13'		1642	1,325	0	0	2	0	0	2
36	0-60	21°24.5'	159°00'		2337	1,385	0	6	5	1	0	12
37	0-60	21°24.5'	158°40'	6/25	0228	1,621	9	8	0	0	0	17
38	0-60	21°25'	158°17'		0526	1,566	1	4	16	0	0	21
64	0	20°43.8'	156°58'	7/11	1924	2,496	0	4	77	0	0	81
65	0	20°42.9'	156°56.5'		2059	2,230	2	10	284	0	7	303
66A	0	20°42.1'	156°55.1'		2301	2,400	0	5	140	0	1	146
66B	0	20°42.1'	156°55.1'		2337	2,864	0	8	173	0	0	181
67	0	20°42.0'	156°53.0'	7/12	0100	2,312	0	5	96	0	0	101
68	0	20°42.0'	156°51.9'		0300	2,343	1	4	65	0	0	70
69	0	20°40.7'	156°50.6'		0501	1,786	4	24	210	0	0	238
71	0-60	20°43.8'	156°55.4'		2001	1,215	0	4	43	0	0	47
72	0	20°42.8'	156°55.5'		2046	2,339	1	22	1,557	0	0	1,580
73	0-60	20°42.2'	156°55.5'		2201	1,626	4	36	186	0	1	227
74A	0	20°42.2'	156°55.6'		2233	2,370	0	11	182	0	0	193
74B	0	20°42.1'	156°56.6'		2306	2,295	4	59	234	0	0	297
75	0-60	20°42.4'	156°58.5'	7/12	2349	1,754	9	11	11	0	4	35
76	0-60	20°44.2'	156°58.3'	7/13	0035	1,587	6	17	138	0	0	161
77	0-60	20°47.2'	157°01.0'		0133	1,434	3	10	36	0	0	49
78	0-60	20°47.1'	157°02.0'		0221	1,646	11	21	65	0	0	97

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

OCEANOGRAPHY OF THE EAST CENTRAL EQUATORIAL PACIFIC AS OBSERVED DURING EXPEDITION EASTROPIC

By THOMAS S. AUSTIN



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ABSTRACT

From September 23 to December 17, 1955, the U. S. Fish and Wildlife Service research vessel *Hugh M. Smith* participated in a multiple-vessel oceanographic survey of the eastern tropical Pacific (Eastropic). The results of physical and chemical oceanographic observations made from the *Smith* are described, with emphasis on those observations and results which are of significance to the distribution and abundance of the marine biota.

OCEANOGRAPHY OF THE EAST CENTRAL EQUATORIAL PACIFIC AS OBSERVED DURING EXPEDITION EASTROPIC

By THOMAS S. AUSTIN, *Oceanographer*
BUREAU OF COMMERCIAL FISHERIES

Since early in 1950, the Pacific Oceanic Fishery Investigations (POFI),¹ U. S. Fish and Wildlife Service, has been studying the oceanography of the central equatorial Pacific. These studies have been centered in an area between 140° W. longitude and the 180th meridian and between 12° N. and 10° S latitude. The work has been directed toward determining circulation features and the associated distribution of the marine chemical and physical factors in order to more adequately understand the variations in the distribution and abundance of the biota, especially the yellowfin tuna (*Neothunnus macropterus* Temminck and Schlegel).

The earlier phases of the program were exploratory. As the resulting data were analyzed, the need for specialized studies became evident. One such study involved the east-west variations in the ecology of the northern boundary of the Equatorial Countercurrent; another, an extension of observations along the Equator to the east of 140° W. longitude. These two studies were carried out during a five-vessel, simultaneous survey of the eastern tropical Pacific (Eastropic). The survey extended from 160° W. longitude to the west coast of the Americas and was conducted during the fall and winter of 1955.

Data and descriptions of the circulation features and distribution of the variables in the general area surveyed during expedition Eastropic are available from several sources. These include, in part, the reports of the *Dana* (Thomsen 1937), the *Carnegie* (Sverdrup et al., 1944; Fleming et al., 1945), the *Albatross* (Bruneau et al., 1953), POFI vessels (see Sette et al., 1954; Austin 1957), and unpublished data kindly furnished by the Scripps Institution of Oceanography (SIO) from their operations Shellback and Capricorn.

The currents in the east-central equatorial Pacific are generally zonal (east-west). They include the westerly flowing North Equatorial Current with its southern boundary near 10° N. latitude, the westerly South Equatorial Current with its northern boundary near 5° N. latitude, and the easterly Equatorial Countercurrent in between. Centered about the Equator and beneath the South Equatorial Current is the easterly flowing Equatorial Undercurrent (Cromwell et al., 1954; Fofonoff and Montgomery, 1955).

Five agencies collaborated in expedition Eastropic. Personnel from POFI aboard the research vessel *Hugh M. Smith* (cruise 31) studied east-west variations in conditions along the northern boundary of the Equatorial Countercurrent and along the Equator. Representatives of SIO and the Inter-American Tropical Tuna Commission aboard the Scripps' vessels, the *Spencer F. Baird* and *Horizon*, operated southward from San Diego, Calif., to northern Peru and in the Gulf of Panama. The *B. S. P. Bondy*, assigned by the Peruvian Hydrographic Office, surveyed off the northwest coast of South America in the general area of the Peru Current, and the California Department of Fish and Game vessel, the *N. B. Scofield*, conducted longline fishing in the area studied by the *Horizon* and the *Baird*. The tracks of all the cooperating vessels are shown in figure 1.

The *Smith* departed Honolulu, Hawaii, on September 23, 1955, on a southerly course, crossed the westerly flowing North Equatorial Current and proceeded into the easterly Equatorial Countercurrent. The boundary between the two currents was determined by the variations in the vertical distribution of temperature (ridge in the thermocline at the northern boundary of the Countercurrent) and the change in direction of flow as shown by the geomagnetic electrokinetograph (GEK) until it became inoperative on

¹ Redesignated Bureau of Commercial Fisheries Biological Laboratory, Honolulu, effective Jan. 1, 1959.

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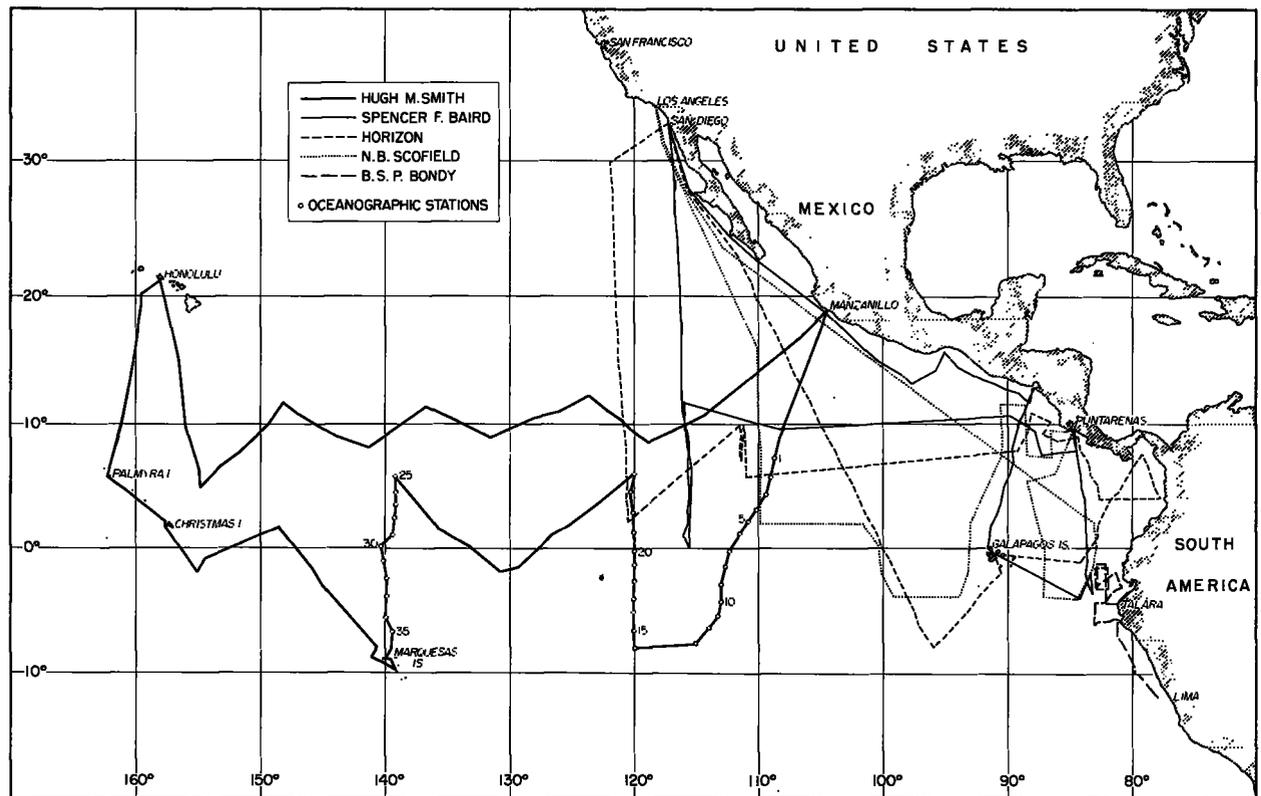


FIGURE 1.—Track chart of vessels participating in expedition Eastropic. Positions of oceanographic stations shown only for *Hugh M. Smith*.

October 10, 1955. The northern edge of the Countercurrent was followed east to 120° W. During this eastbound leg of the cruise, bathythermograph (BT) lowerings were made at 2-hour intervals and surface samples were collected twice daily for inorganic phosphate and salinity determinations. The vessel then proceeded to Manzanillo, Mexico, for refueling and supplies.

The *Smith* departed Mexico on October 24, 1955, on a generally southwesterly course across the coastal currents, the Countercurrent, and to 8° S. latitude in the South Equatorial Current. The westward passage was planned in order to study the equatorial divergence and the associated oceanographic and biological events. A series of standard oceanographic casts to 1,200 meters was made at approximately 90-mile intervals, between 6° N. and 8° S. latitude near 110° W., along 120° W., and along 140° W. longitude. The northernmost station of the 110° W. leg was in the Countercurrent. The rest of the stations were in the westerly flowing South Equatorial Current.

Bathythermograph lowerings were made at each station and at 2-hour intervals between stations. Surface phosphate and salinity samples were taken at frequent intervals.

The data resulting from the observations and collections taken by the *Smith* during expedition Eastropic have been published by King, Austin, and Doty (1957); those from the *Baird* and the *Horizon* by the University of California (1956). Both of these publications include tabulations of the observed data and a description of the sampling and analytical methods used aboard the vessels. The report of King et al. also includes oceanographic station curves, tabulations of the biological data and a description of the methods used in the shore-based processing and analyses.

The purpose of this paper is, primarily, to describe the oceanic circulation features and the associated distribution of variables as determined from the data collected by the *Smith*, particularly those features having significant influence on the distribution and abundance of the biota. Data

from other participating vessels and those from previous surveys to the Eastern Central Pacific, both by POFI and other agencies, will be used as needed.

RESULTS OF OCEANOGRAPHIC OBSERVATIONS

We shall, in general, describe the results of the oceanographic program of the *Smith* in the following order: The general circulation, the vertical distribution of variables, their horizontal distribution, and finally, a discussion of the significance of the circulation features to the distribution and abundance of the biota. In each section we shall describe first the conditions in the Countercurrent, then those in the South Equatorial Current; the latter with particular attention to conditions along the Equator.

CIRCULATION FEATURES

As an introduction to the discussions of the observed vertical and horizontal distribution of the oceanographic properties, we shall first describe the general circulation features for the area and period of the *Smith* cruise. The direction of flow normal to the three oceanographic sections (henceforth referred to as 110° W., 120° W., and 140° W.) was determined by means of geostrophic calculations. Inferences as to direction in the region of the Countercurrent and elsewhere in the area where density data were lacking, were made from variations in the temperature-depth distribution. Information on variations in velocity was derived from changes in wire angles between successive Nansen-bottle casts. Frequent references will be made to the results of the GEK measurements made aboard the *Baird* and the *Horizon*.

The geopotential anomalies were computed, with pressure terms neglected, directly from the oceanographic station graphs (see King et al., 1957, fig. 9). The average values of thermosteric anomaly for depth intervals of 100 meters in the deeper layers and 10 meters in the thermocline and mixed layer, were multiplied by the pressure interval in decibars and then were summed upward from the 700-db. level. The 700-db. surface was used as the reference level since the bottom bottle on several stations was down less than 800 meters due to large wire angles.

In figure 2, the heights of the sea surface in dynamic centimeters (as calculated from the stations along 110°, 120°, and 140° W.) have been contoured relative to the 700-db. surface. The configurations of the isopleths for the geopotential anomaly between the three longitudes were drawn from consideration of the temperature-depth data. The inferred direction of flow is shown by the heavy arrows.

The station-to-station variation (meridional slope) of the 0/700-db. surface for each of the three sections is shown in figure 3. The slope, indicative of the speed of westerly flow, is steeper between the Equator and 5° N. on the 110° W. and 120° W. sections being, respectively, 0.28 and 0.42 dynamic meters in 570 km. This is to be compared with 0.07 dynamic meter over the same distance along 140° W. The surface velocities relative to the 700-db. level (as well as the velocities for the remainder of the *Smith* sections) are given in the following table. As the geostrophic approximation is not considered applicable near the Equator, relative velocities between 3° N. and 3° S. have not been calculated.

Latitude	140° W.		120° W.		110° W.	
	Speed (knot)	Direction	Speed (knot)	Direction	Speed (knot)	Direction
7° N-6° N					0.2	E
6° N-5° N			0.4	W	.4	W
5° N-4° N	0.1	W	2.3	W	.7	W
4° N-3° N	.2	W	1.8	W	.8	E
3° S-4° S	.6	W	.2	W	.4	E
4° S-5° S	1.0	W	.8	W	1.1	W
5° S-6° S	.3	W	.7	W	.5	E
6° S-7° S			.3	W	.6	W

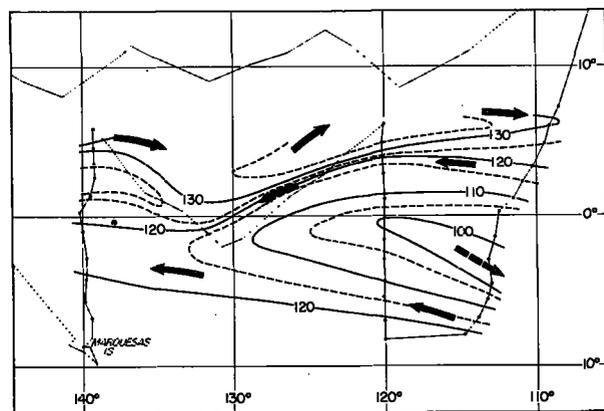


FIGURE 2.—Variations in the geopotential topography, 0/700-db. surface as calculated from Eastropic data. The arrows denote the direction of flow. (Contour interval, 5 dynamic centimeters.)

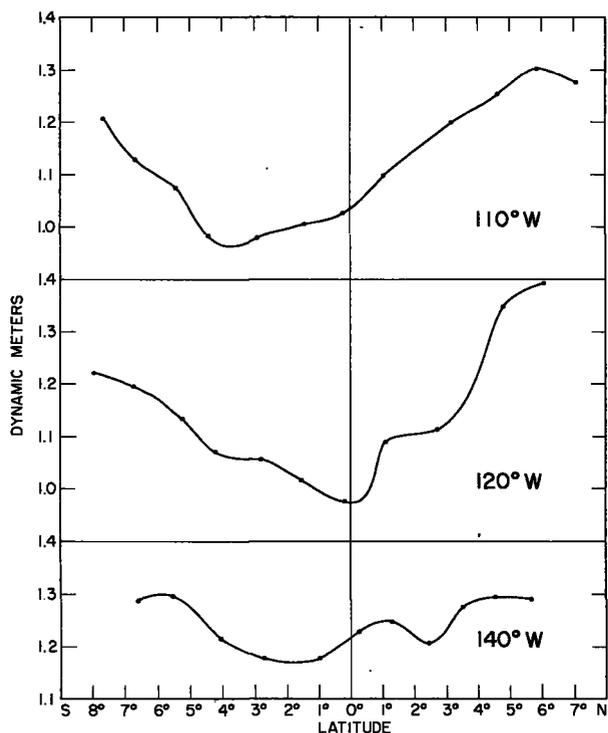


FIGURE 3.—Station-to-station variations in the geopotential topography (0/700-db. surface) for the *Hugh M. Smith*, 110° W., 120° W., and 140° W. sections.

Unfortunately, the *Smith* was not equipped to make direct measurements of velocities for these transects. Surface currents measured by the GEK aboard the *Horizon* (University of California, 1956), 5°09' N. to 2°11' N. latitude, near 120° W. longitude (October 11 and 12, 1955), varied between 0.86 knot (323° T.) at 2°48' N. and 2.0 knots (324° T.) at 3°08' N., the latter value being measured near a marked temperature discontinuity (front). The contours in the region of the front (fig. 2), also encountered by the *Smith* (near 4° N., 120° W.), are rather closely spaced reflecting the comparatively swift westerly flow measured by the *Horizon*. The *Baird*, near 115° W. longitude and between the same limits of latitude, observed velocities between 1.1 knots (063° T.) at 5°02' N. and 5.7 knots (288° T.) at 0°43' N. As can be seen from table 1, the calculated relative velocities for the *Smith's* survey did not exceed 2.3 knots (3° N.—4° N. along 120° W.).

Referring to figure 3, the break in slope near the northern limit of the 110° W. section suggests the northernmost station was in the Countercurrent. The lack of a break in slope between the

two northernmost stations of the 120° W. and 140° W. sections suggests these sections did not reach into the Countercurrent. In the southeastern portion of the survey area, the geostrophic considerations yield an easterly flow centered about 2° S. latitude (fig. 3, 110° W. section). The trough normally centered at or very near the Equator is, in this instance, positioned at 4° S. latitude.

Indirect evidence of the easterly flow in the surface waters, 1° S. to 4° S., is to be found in the wire-angle data for the Nansen bottle casts. Along the 110° W. section, the angles near to and north of the Equator (to 4°30' N.) were large, 50° to 60° from the vertical. These large angles were the cumulative effects on the wire of the easterly winds on the vessel, the westerly surface flow and the decrease in velocities at the subsurface levels penetrated by the cast. Between 1° S. and 4° S., with 11- to 15-knot easterly winds, the angles fell to less than 10° (06° at 1°23' S. and 03° at 2°54' S.). The easterly surface flow exerted a "canceling effect" on the vessel and the wire angles thus were very small.

On both 110° W. and 120° W., there was an appreciable change in wire angle near the front, with smaller angles to the north of the front (10°) and larger angles to the south (50°). These differences in angle reflect the differences in velocity of the surface waters. The two stations on 120° W. nearest the front were station 22, approximately 90 miles to the south of the front, and station 23, approximately 30 miles to the north of the front. Referring to velocity measurements made aboard the *Horizon* (University of California, 1956), the speed of the surface flow decreased from near 4 knots in waters to the south of the front to 1 knot or less in those to the north. Considering that most of the Nansen bottles and wire were in deeper waters of low velocities, the comparatively swift surface currents south of the front would result in such large wire angles.

VERTICAL DISTRIBUTION OF PROPERTIES

Temperature

Temperature sections along selected longitudes (120° W. to 160° W.), each crossing the main features of the equatorial zonal circulation in the central Pacific, have previously been published in POFI oceanographic and biological reports (i.e., Cromwell 1954; Stroup 1954; Austin, 1954a and

1954b; and Murphy and Shomura, 1953). During Eastropic, no single leg of the *Smith's* track provided data for such a section. Therefore, in figure 4, two BT sections, one near 155° W. from 15° N. to 5° N. and one along 140° W. between 5° N. and 8° S. are used to illustrate the north-south temperature-depth distribution. The 60°, 70°, and 80° F. isotherms were drawn with the 72° and 74° F. isotherms included near the Equator.

From north to south (right to left in fig. 4, A) in the North Equatorial Current, the isotherms slope upward, reaching a minimum depth at the northern boundary of the Countercurrent, then slope downward to the southern boundary of the Countercurrent. This interpretation of the current boundaries is based on the assumption of geostrophic flow. In the next section (fig. 4, B), 140° W., 4° N. to 4° S., both the upward trend of the isotherms toward the Equator and their deepening south of the Equator, compatible with westerly flow, are discernible. Various mixing processes at or near the Equator resulted in the "irregularities" which mask the ridge expected from the distribution of mass when a westerly flow is centered about the Equator.

The mixing of the cooler subsurface waters with those at the surface near the Equator is reflected in the configuration of the 74° F. isotherm, which intersects the surface to the north and to the south of the Equator. A trough in the isotherms centered beneath the Equator is suggested in figure 4, but it is not as evident as generally found in meridional sections crossing the Equator in the central

Pacific (Austin 1954b; Wooster and Cromwell, 1958).

The 60° and 70° F. isotherms at the southern limit of the 155° W. section (fig. 4, A) are about 50 meters deeper than those at the northern limit of the 140° W. section. This difference results from the rapid east-west deepening of the thermocline between 125° W. and 160° W. longitude.

To illustrate this deepening, temperature-depth data from BT's taken at eight positions along the Equator, 112° W. to 156° W. longitude, have been contoured in figure 5. Near 155° W., the top of the thermocline is at 150 meters, decreasing in depth to 50 meters near 125° W., then deepening slightly toward the eastern end of the section.

Other features in the temperature-depth distribution of the three meridional sections warrant attention. Of the sections that crossed the Equator (see fig. 1), three were made along courses nearly normal to the Equator. The temperature-depth profile for each of these sections is shown in figure 6, A (110° W.), 6, B (120° W.), and 6, C (140° W.). In all three, the well-developed two-layer system, characteristic of tropical waters, is evident. The principal variation among the three sections is in the depth of the thermocline.

Along the 110° W. section (fig. 6, A), there is a gradual decrease in depth of the thermocline from 5° N. latitude south across the Equator to 4° S. latitude. This suggests that between 0° and 4° S. there is a reversal in flow with the surface waters directed to the east, becoming westerly again south of 4° S. Two centers of cold water at

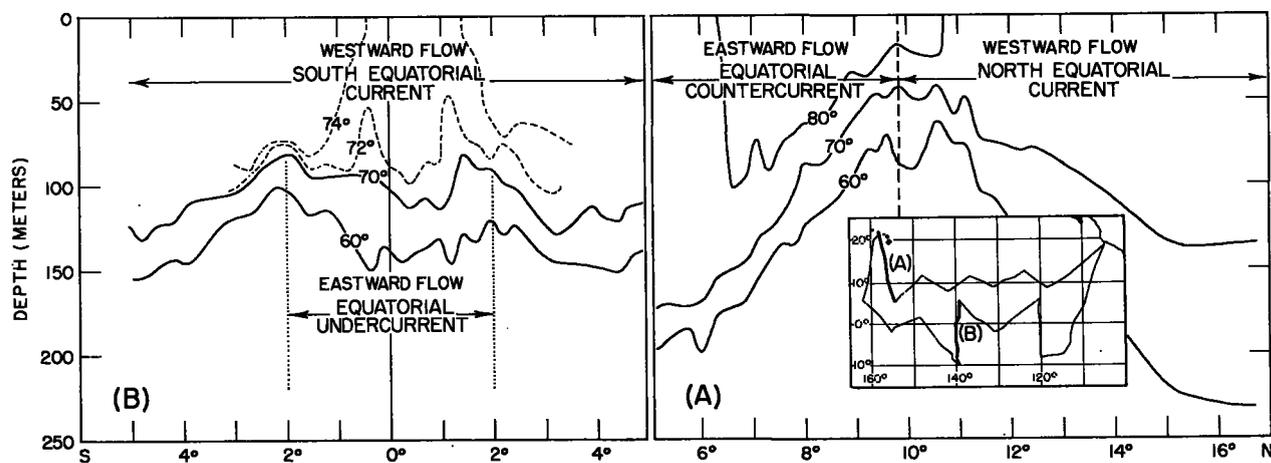


FIGURE 4.—Vertical temperature (°F) section from Eastropic BT records: composite of such records along 140° W. and 155° W. longitude.

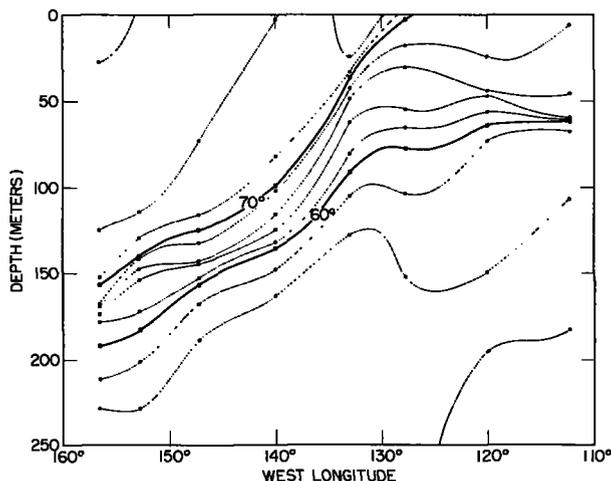


FIGURE 5.—Vertical temperature ($^{\circ}$ F.) distribution along the Equator illustrating the east-west slope of the thermocline.

the surface are shown. One center near the Equator and similar to that described for the 140° W. section (fig. 4) results from the effects of the wind-induced divergence and upwelling. At the second, near 4° S., the shallow thermocline, coupled with mixing by the wind and by the turbulence at the interface of the opposing easterly and westerly surface currents, results in cooler water at the surface.

The second meridional section, that along 120° W., is shown in figure 6, B. Within the comparatively short span of the section, 6° N. to 8° S., the thermocline approximates a dome with its center positioned at the Equator. Near the northern end of the section, the isotherms show a reversal in slope, decreasing in depth to either side. This trough undoubtedly approximates the position of the southern boundary of the Countercurrent. The domed configuration over the rest of the section reflects the flow of the westerly South Equatorial Current.

Near 4° N. latitude, 120° W. longitude, the isotherms (70° to 76° F.) abruptly descend from the surface. It was near here that the *Smith* crossed a marked front such as that encountered during a previous cruise to this area (Cromwell and Reid, 1956). A temperature-depth section drawn from BT data taken at and within a few miles either side of the front is shown in figure 7. One BT (No. 447), taken with vessel underway at 2 knots, was sufficiently close to the front so

that the "up" and "down" traces in the first 20 meters differed by 3° F., and could be used as a reference to locate the position of the other BT records relative to the front. Following Cromwell and Reid (1956, figs. 3 and 4), the waters which were "nearly isothermal" have been shaded in figure 7.

The Scripps vessel, the *Horizon*, observed a similar feature 1 month later near 3° N. latitude, 120° W. longitude (Knauss 1957). Knauss interprets the circulation at the front as "cold water overrunning the less dense warm water and then plunging downward." He describes the feature as a "cold front" with the cold water to the south moving at right angles to the front at speeds in excess of 2 knots.

Along the 140° W. section (fig. 6, C), the decrease in temperature per unit of depth through the thermocline is less than in the previous two sections (110° W. and 120° W.), and the thermocline, 4° N. to 4° S., is 50–75 meters deeper. The influence of the Equatorial Undercurrent on the vertical temperature distribution is suggested between 2° N. and 2° S. latitude. With westerly surface flow along the Equator, a ridge centered near the Equator is expected. North and south of 2° N. and 2° S., respectively, the thermocline shows an upward trend toward the Equator. Between these two latitudes is a trough; i.e., warmer waters at greater depths. This trough may be interpreted as the result of advection of the warmer waters from the west into the lower part of the surface layer and to an unknown depth into the thermocline (Fofonoff and Montgomery, 1955). A similar situation, vertical spreading of the isotherms, may be seen (2° N. to 2° S.) on the 120° W. section (fig. 6, B) and to a lesser degree on the 110° W. section (fig. 6, A). On the latter section, however, is a southerly displacement of the trough, undoubtedly related to the easterly surface flow south of the Equator (1° S. to 4° S.). Further details of the 140° W. vertical temperature section were discussed in connection with figure 4.

Salinity

The most prominent feature in the subsurface distribution of this variable is the tongue of high salinity water south of the Equator at a depth of about 150 meters (fig. 8). In comparing the salinities in this feature on the three sections, there

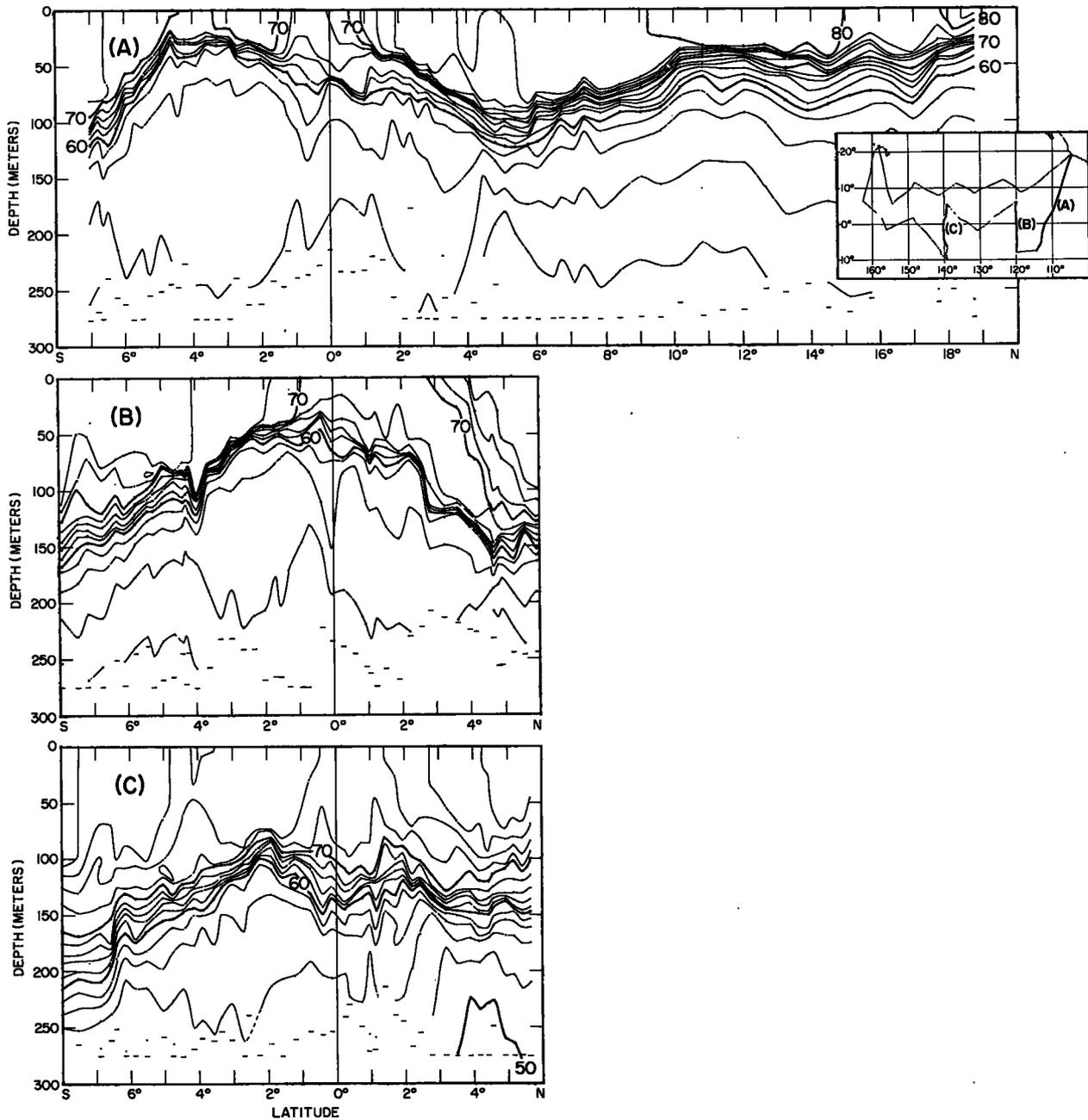


FIGURE 6.—Bathythermograph temperature-depth sections 110° W. longitude (A); 120° W. longitude (B), and 140° W. longitude (C). Contour interval 2° F. (from King et al., 1957).

is a progressive increase, east to west, from 35.30 ‰ to 35.80 ‰ to a maximum of 36.13 ‰. From east to west there is an increasingly apparent northward extension of the tongue.

The source of these higher salinity waters at an intermediate level is a Southern Hemisphere salinity maximum in the surface waters positioned

near 20° S., extending east to west between approximately 100° W. and 140° W. (Fleming et al., 1945, fig. 292). In this region of descending flow of air in the atmosphere above the ocean and associated evaporation from the sea surface, more saline waters are formed and sink, moving northwesterly then westerly at subsurface levels. The

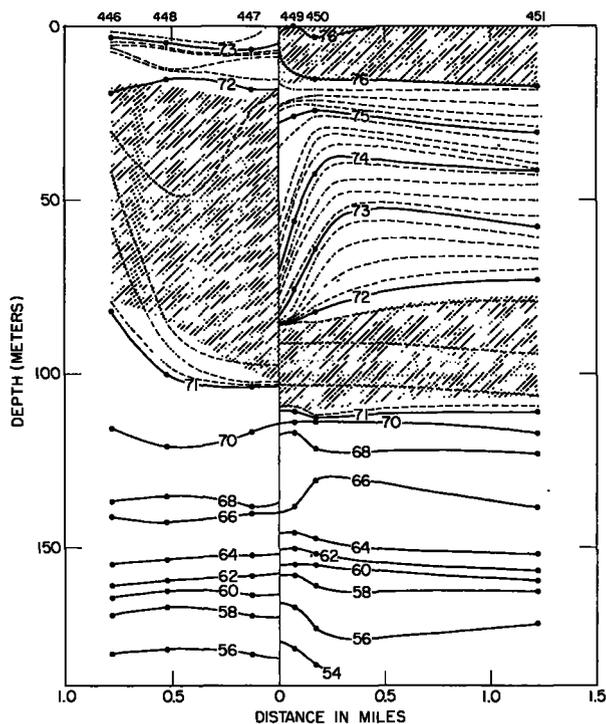


FIGURE 7.—Vertical distribution of temperature ($^{\circ}$ F.) across the front observed by the *Smith* near 4° N. latitude, 120° W. longitude.

relation between the position of the surface salinity maximum and the subsurface trajectory is reflected in the variations in the feature on the three longitudes (fig. 8); i.e., its northern extent ends abruptly near the Equator in the central and east-central Pacific. This was shown in previous POFI sections by Cromwell (1954), Austin (1954a, 1954b), Stroup (1954), Montgomery (1954), and by Fleming et al. (1945, figs. 119 and 143). Austin (1954b, fig. 21) has shown by the temperature-salinity characteristics that this abrupt termination of the salinity maximum at the Equator in the eastern Pacific is associated with the vertical mixing processes accompanying upwelling. In contrast, in the western Pacific the maximum penetrates into the Northern Hemisphere, reaching at least 5° N. (Mao and Yoshida, 1955). Austin and Rinkel (in press) suggest that this is evidence for less-intensive upwelling in the western Pacific.

Comparison of the temperature/salinity (T/S) characteristics for the Eastropic stations along 110° and 120° W. also reveals the longitudinal variation in the subsurface salinity maximum and

the rather abrupt change near the Equator. Along 110° W. (fig. 9, A), the T/S curves south of the Equator all show a rapid subsurface decrease in temperature with small change in salinity. Similar curves for the stations along 120° W. (fig. 9, B) show a configuration for those stations south of the Equator which is attributable to the subsurface maximum. On the T/S curve for the first station north of the Equator (station No. 21), $1^{\circ}06' N.$; 120° W., the Southern Hemisphere maximum is no longer in evidence.

Returning to figure 8, we note that the waters in the surface layer near the northern limits of the three sections, particularly those along 110° W. and 120° W., are characterized by low salinities. Along 110° W., the salinities in the surface layer are below 34.00 ‰ (a minimum of 33.49 ‰) at the northern two stations ($07^{\circ}06' N.$ and $05^{\circ}52' N.$). Westward along similar latitudes, there is a gradual increase to 34.47 ‰ on the 120° W. section and 34.72 ‰ on 140° W. These low salinities are attributable to dilution by rainfall and influence of waters moving in from the east and northeast. As shown by Schott (1935), a ridge of mean maximum rainfall is centered along 10° N., becoming increasingly prominent to the east and reaching a maximum in the Gulf of Panama. East of the *Smith's* survey area, as revealed by the *Carnegie* data (Fleming et al., 1945, fig. 222) and by data taken aboard the Scripps Institution of Oceanography vessels during Eastropic (University of California, 1956), the salinities in the surface waters progressively decrease, reaching minimal values of 29.50 ‰ to 30.00 ‰ in the Gulf of Panama (3° – 6° N. latitude).

In the deeper waters sampled during expedition Eastropic, at 500–1,000 meters, the salinities were those characteristic of the Antarctic intermediate waters with the axis of the lowest values rising toward the north on each section (King et al., 1957, figs. 11, 16, and 21).

Density

The vertical distribution of density along each of the three sections, expressed as thermosteric anomaly in centiliters per ton (following Montgomery and Wooster, 1954), is shown in figure 10. The most striking feature on each of the three sections is the rapid increase in density with depth (which we shall refer to as the stable layer)

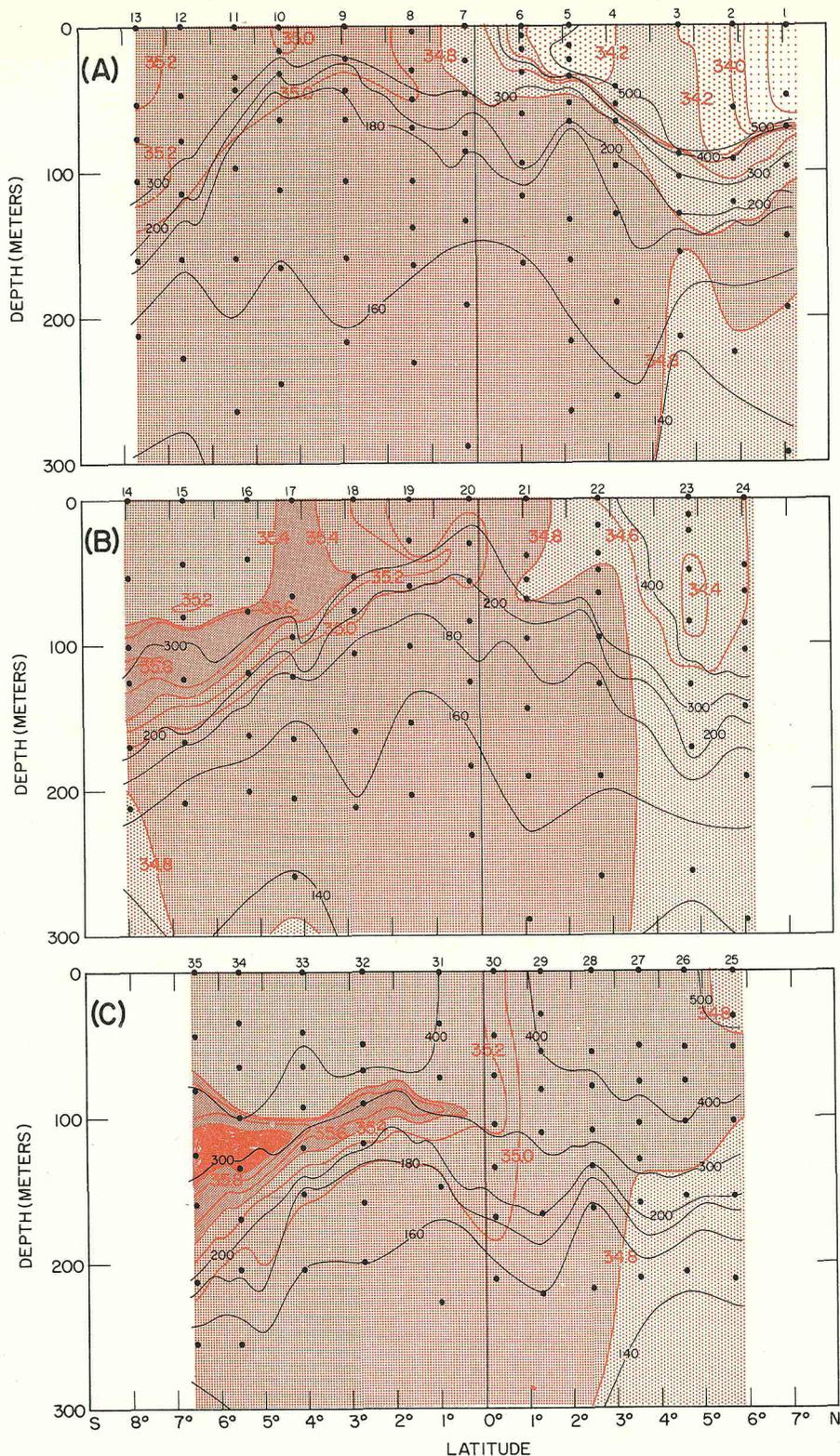


FIGURE 8.—Vertical distribution of salinity (‰) along 110° W. (A), 120° W. (B), and 140° W. (C). Contour interval 0.2 ‰ (from King et al., 1957). Density isopleths in black (in centiliters per ton). Depths of observations are shown by dots; station numbers are given along the top of each panel.

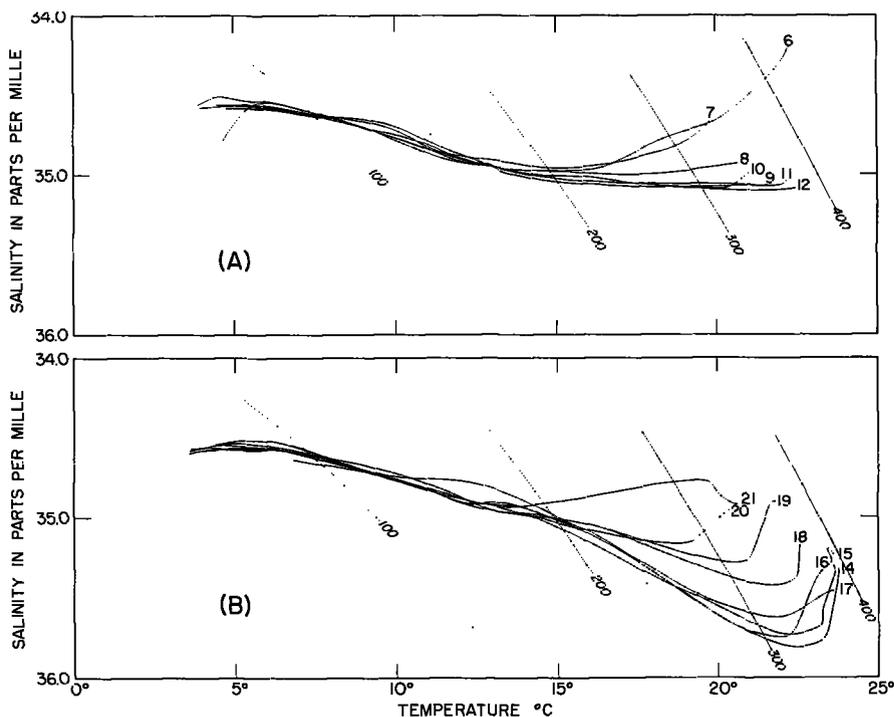


FIGURE 9.—Temperature ($^{\circ}$ C.)-salinity (‰) curves at selected stations, Southern Hemisphere along 110° W. (A), 120° W. (B). Density (oblique lines) in centiliters per ton.

through the thermocline. Although variations in salinity, as well as temperature, affect the vertical distribution of density of sea water, in tropical waters salinity usually plays a minor role. To illustrate: from east to west (particularly between the 120° W. and the 140° W. sections) there is a general increase in depth of both the thermocline and the stable layer. There is a trough in each at the southern boundary of the Countercurrent and a marked ridge near the Equator on 140° and 120° W., and near 4° S. on 110° W. The change in temperature and density across the front is reflected in the "bunching" of the density isopleths at their intersection with the surface near 4° N. on 120° W. and 1° N. on 110° W.

Oxygen

The vertical distribution of oxygen is shown in figure 11. Selected isopleths for δ_t are shown on each section. On the four longitudes, the oxygen content in the surface layers, surface to the top of the thermocline, was uniformly high, 4.0 to 5.5 ml./L., decreasing through the thermocline to the oxygen minimum, then increasing to maximum depths sampled. Near 100° W. and 110° W., the

minimum with values of less than 0.5 ml./L. was continuous from the Southern to the Northern Hemisphere. Along the 120° W. and 140° W. sections, values less than 0.5 ml./L. were observed only in the Southern Hemisphere. On each section a narrow, vertical tongue of water with higher oxygen content was centered beneath the surface waters at the Equator.

The low oxygen values in the minimum south of the Equator (300–500 meters) are in waters which have moved westerly from the coast of Peru and, at least in part, result from the consumption of oxygen at subsurface depths by decomposition of the organic material which was in these waters when they departed from the surface and of the organic detritus sinking from the euphotic zone.

North of the Equator in the eastern Pacific is a large subsurface body of water within which the oxygen content is low (0.1 ml./L. or less). As described by Sverdrup et al. (1942, p. 729), this body of water is found off the American coast between 28° N. and the Equator, extending to the west as far as 140° W. More recent data (Cromwell 1951) bring this westward extension to at least 172° W. The lowest oxygen concentrations,

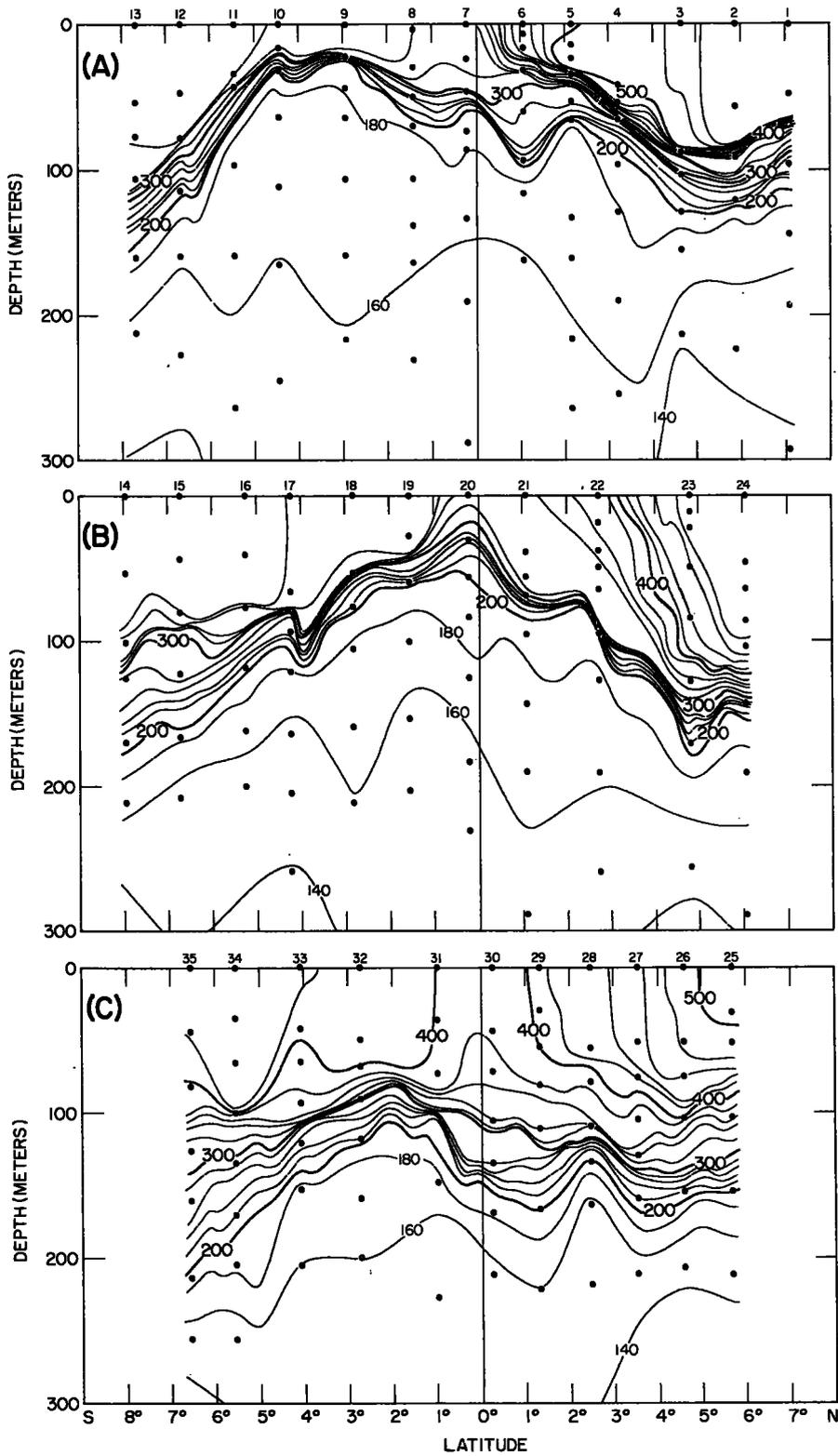


FIGURE 10.—Vertical distribution of density expressed as thermosteric anomaly along 110° W. (A), 120° W. (B), and 140° W. (C). Contour interval 20 centiliters per ton (from King et al., 1957). Depths of observations are shown by solid dots; station numbers are given along the top of each panel.

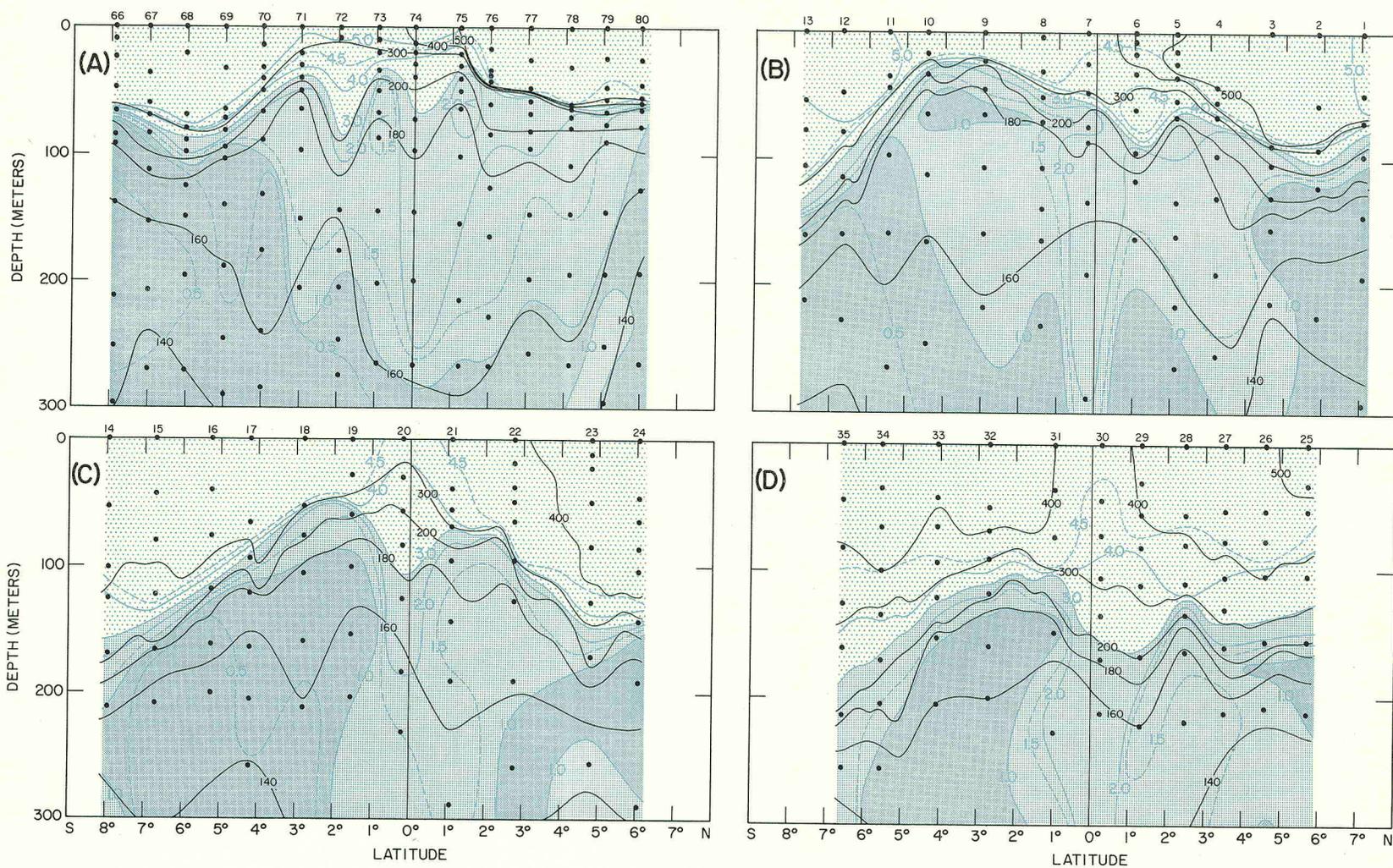


FIGURE 11.—Vertical distribution of oxygen expressed in milliliters per liter (ml./L.) along sections near 100° W. (A), 110° W. (B), 120° W. (C), and 140° W. (D). Contour interval 0.5 ml./L. (data for A from University of California, 1956; B, C, and D modified from King et al., 1957). Depths of observations are shown by dots; station numbers are given along the top of each panel.

without separating the double minima, have been contoured in figure 12. Values equal to or below 0.1 ml./L. have been shaded. The values in the minimum near the Equator are somewhat higher than those to the north or to the south.

Phosphate

The Automatic Servo-Operated Photometer used for the determination of inorganic phosphate broke down at station 8 along the 110° W. leg. Subsequently, samples were frozen from selected depths at the remainder of the stations along this leg, and at less frequent depth intervals (surface to 200 m.) along 120° W. The meridional sections resulting from these data are shown in figure 13.

Along 110° W., the phosphate concentrations in the mixed layer were low (0.4 $\mu\text{g. at./L.}$ or less) between the northern limit of the section (7° N.) and about 2° N. The values progressively increased to a maximum of slightly more than 1.0 $\mu\text{g. at./L.}$ at about 3° S., then decreased to less than 1.0 from 5° S. to the southern limit of the section (8° S.). Values in the mixed layer were also low (0.4 $\mu\text{g. at./L.}$ or less) at the northern stations of the 120° W. section, but increased suddenly (0.4 to 1.0 $\mu\text{g. at./L.}$) upon crossing the front near 4° N. The highest values in the surface waters were near the Equator (1.2 $\mu\text{g.}$

at./L.), decreasing to less than 1.0 $\mu\text{g. at./L.}$ near 1° S. and remaining less than this value to 8° S.

Comparison of the phosphate concentrations in the mixed layer of the two sections reveals the association of this nonconservative property with the previously discussed vertical distribution of density (the thermocline) and zonal flow. In the northern portions of the sections, the low phosphate concentrations are in the impoverished waters of the Countercurrent. Near the Equator on 110° W., some enrichment results from upwelling, but the highest values on this section, near 4° N., result from the very shallow thermocline and wind "plowing" (Sverdrup 1952) into the deeper, nutrient-rich waters. Near the Equator on 120° W., the surface enrichment probably results primarily from upwelling. The northern transport of these waters is reflected in the higher phosphate values, from the Equator north to the latitude of the front.

HORIZONTAL DISTRIBUTION OF PROPERTIES

Although this section will deal primarily with the surface distribution of temperature, salinity, and phosphate, we shall, as necessary, include concurrent consideration of the vertical distribution of the property in question. The direction of the flow, as determined by geostrophic calculations (see fig. 2) has been reproduced on the charts.

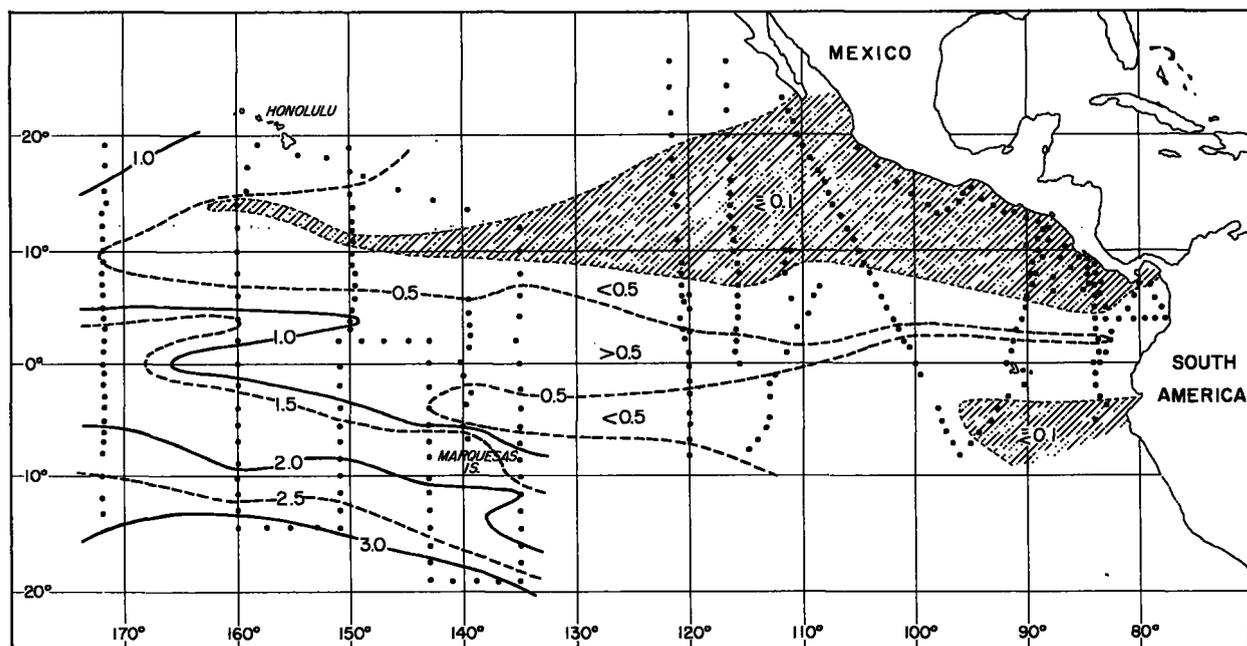


FIGURE 12.—Concentrations in the oxygen minimum. (Data from POFI and Scripps cruises.)

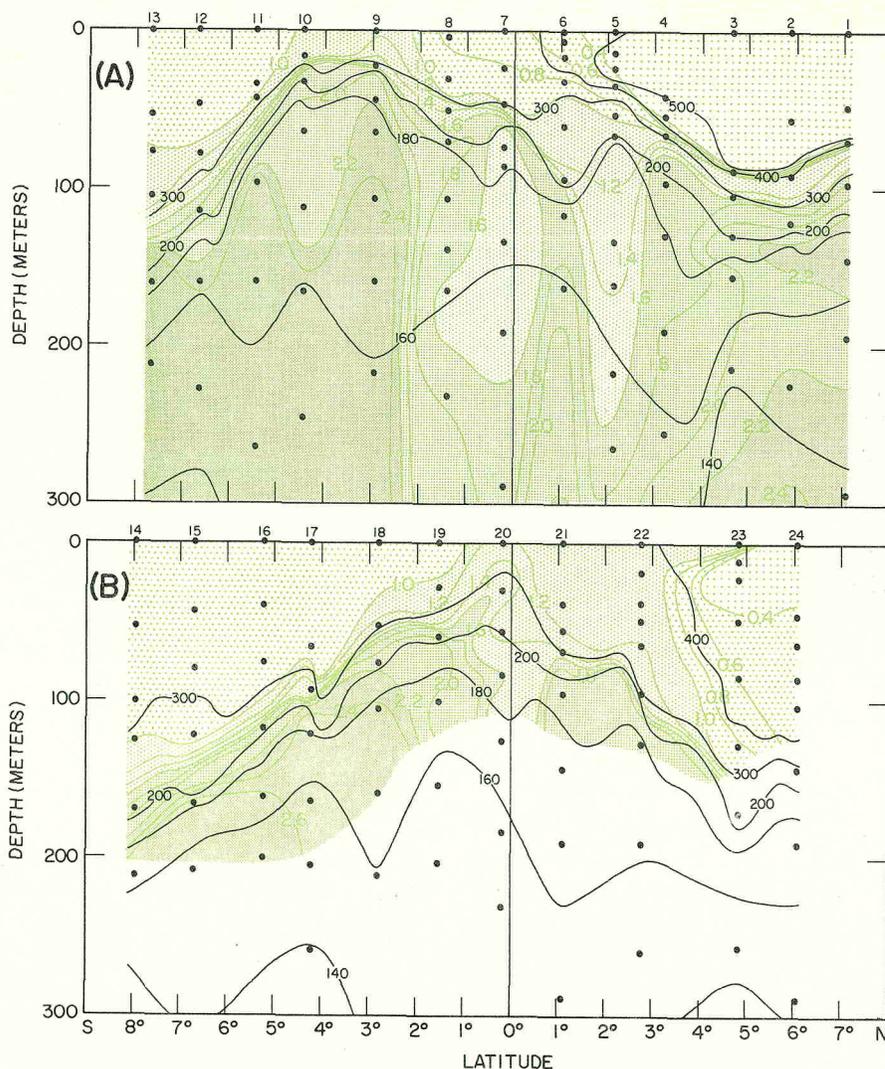


FIGURE 13.—Vertical distribution of phosphate expressed in microgram-atoms per liter ($\mu\text{g. at./L.}$) along sections near 110° W. (A) and 120° W. (B). Contour interval $0.2 \mu\text{g. at./L.}$ (from King et al., 1957). Depths of observations are shown by dots; station numbers are given along the top of each panel.

Surface Temperature

The surface temperatures, as measured in the bucket samples taken at each BT lowering (generally at 2-hour intervals, 15 to 20 miles apart) are shown by the black contours in figure 14. Mean surface temperature distribution for the month of November, as published in an atlas prepared by the British Air Ministry (1950), is shown by the red contours.

In the Countercurrent (5° N. to 10° N. latitude) there is general agreement between the Eastropic surface temperatures and the mean. Over most of the area the 80° F. isotherms in each case straddle

the somewhat warmer waters in the center of the current, but swing northerly from the latitude of the axis in the eastern part of the survey area. This northerly shift in position of the isotherms reflects the influence of the warmer waters moving to the west away from the coast of Central America. A similar configuration of the surface isotherms is evident in the report by Jerlov (1956, fig. 3) describing the results of the Swedish *Albatross* expedition to the same area and during the same months (October–November 1948).

The distribution of surface temperatures (also salinity and phosphate) suggests that there was a southerly bulge in the Countercurrent centered

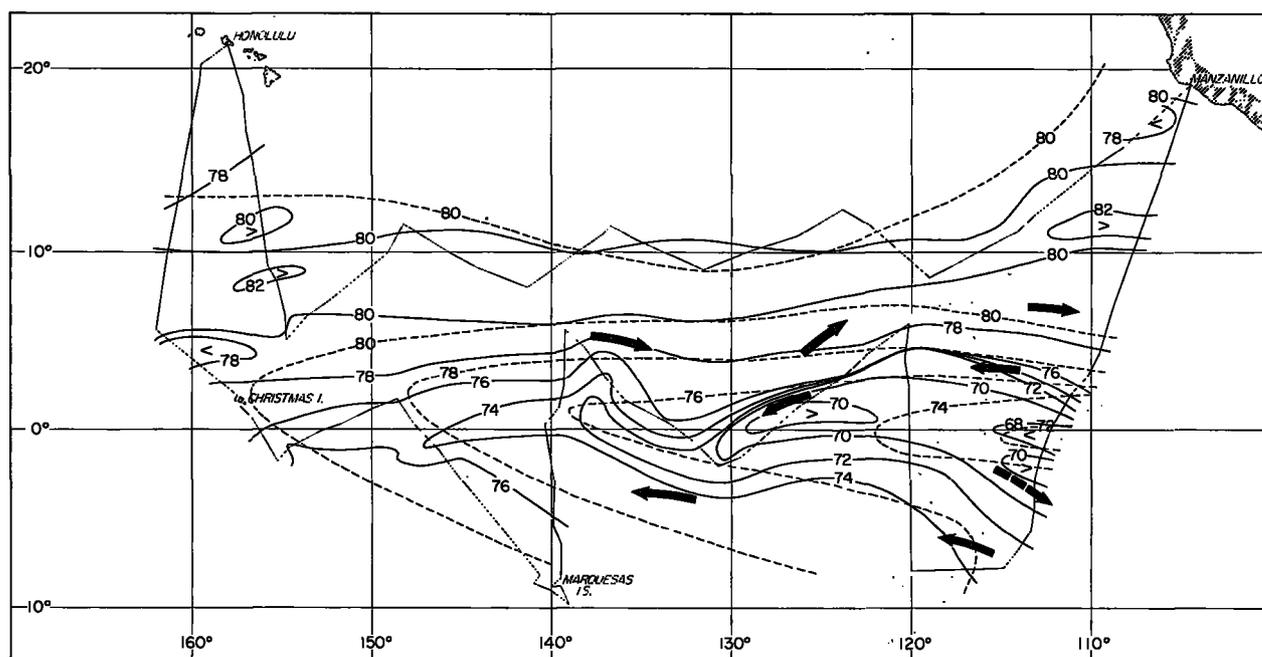


FIGURE 14.—Surface temperature ($^{\circ}$ F.) distribution from temperatures of bucket samples taken at position of BT lowerings in black; mean temperatures from British Air Ministry Atlas (1950) in red. The arrows denote current direction as determined from geostrophic calculations.

near 132° W. longitude. Although this feature appears to be real, there is the possibility that it is an artifact resulting from the V-shape of the vessel track in this area. There is an acceptable comparability, however, in the shape of the contours defining the bulge among all the surface variables measured. Similar variations were reported by Cromwell (1956, p. 29) during expedition Eastropic.

The cooler surface temperatures in the South Equatorial Current, particularly along the Equator, are strikingly evident. In fact, those observed near the Equator during the period of Eastropic were from 2° to 4° F. cooler than the mean. At any point along the Equator, these cooler waters reflect both the mixing of the deeper waters with those at the surface and, in varying degrees, advection from the east. The mixing involves at least two separate physical processes, one related to the divergence of the surface waters under the influence of winds with an easterly component, the other, mixing by the wind which is more effective in the east because of the west-to-east shoaling of the thermocline. At present, quantitative estimates of the relative roles of each of these two processes are not available.

The oceanic front described in earlier sections was evident near 4° N. latitude on 120° W. longitude, across which there was an abrupt change in surface temperature of nearly 4° F. (fig. 14). This circulation feature was discernible in varying degrees near 4° N., 135° W. and 2° N., 112° W. That it may be a semipermanent feature in this region of the Pacific is evidenced by the fact that during expedition Eastropic the Scripps vessel, the *Horizon*, observed it 1 month later than did the *Smith* (Knauss 1957), and a similar feature was previously detected by the *Smith* near 1° N., 120° W. on October 27, 1952 (Cromwell and Reid, 1956). However, a front was not detected by the *Albatross* during October–November 1947 when she crossed the Equator at 137° W. (Jerlov 1956, p. 150), nor by the *Baird* which was working during expedition Eastropic only 300 miles to the east of the *Horizon* (Knauss 1957).

Depth of Thermocline

From the preceding discussion of the distribution of temperature, it is evident that there was considerable variation in depth of the thermocline throughout the area surveyed by the *Smith*. The

thermocline depths, as read from the BT slides, have been plotted and contoured in figure 15.

On and near the Equator an objective determination of the thermocline depth is generally difficult since in this region there often is either more than one inflection of the curve or a continuous negative gradient from the surface to the maximum depth of the BT trace (fig. 16). In both figures 15 and 16 this region has been indicated by shading, and the contours in figure 15 have been terminated at their points of intersection with the northern and southern boundaries of this region. This was done because there is a question as to whether or not the two well-defined thermoclines, one south of the Equator and one to the north, are the result of the same physical processes.

Certain inferences to the circulation features may be drawn from the spacing and configuration of the contours in figure 15. The northern boundary of the Countercurrent was coincident with the ridge near 10° N. (<100 ft.) and the southern boundary was centered along the trough in the thermocline depth near 5° N. latitude. In the southeastern portion of the area, a second ridge is evident at about 4° S. latitude. This reflects the distribution of mass associated with easterly flow

there (see the results of the geostrophic calculations in fig. 3).

Surface Salinity

The lowest surface salinity values (fig. 17) were measured along the northern boundary of the Countercurrent, with the minimal value (33.6 ‰) being near 10° N., 128° W. This distribution reflects the extension of low salinity water westward from the coast of Central America and is also coincident with the zonal band of high rainfall located near 10° N. (Schott 1935, plate XIX).

As the *Smith* proceeded south across the Countercurrent and into the South Equatorial Current, surface salinity generally increased, reaching the maximum observed values at the southern extremities of the *Smith's* tracks. Somewhat farther south (near 20° S. latitude) was the southeastern Pacific salinity maximum, with surface values of 36.00 ‰ or greater (Sverdrup et al., 1942, chart VI).

Near the front, the configuration of the isohalines showed an abrupt discontinuity in salinity, with higher salinity water, reaching 34.9 ‰, on the northern side of the front and surface waters with lower salinity, 34.2 to 34.4 ‰, to the south

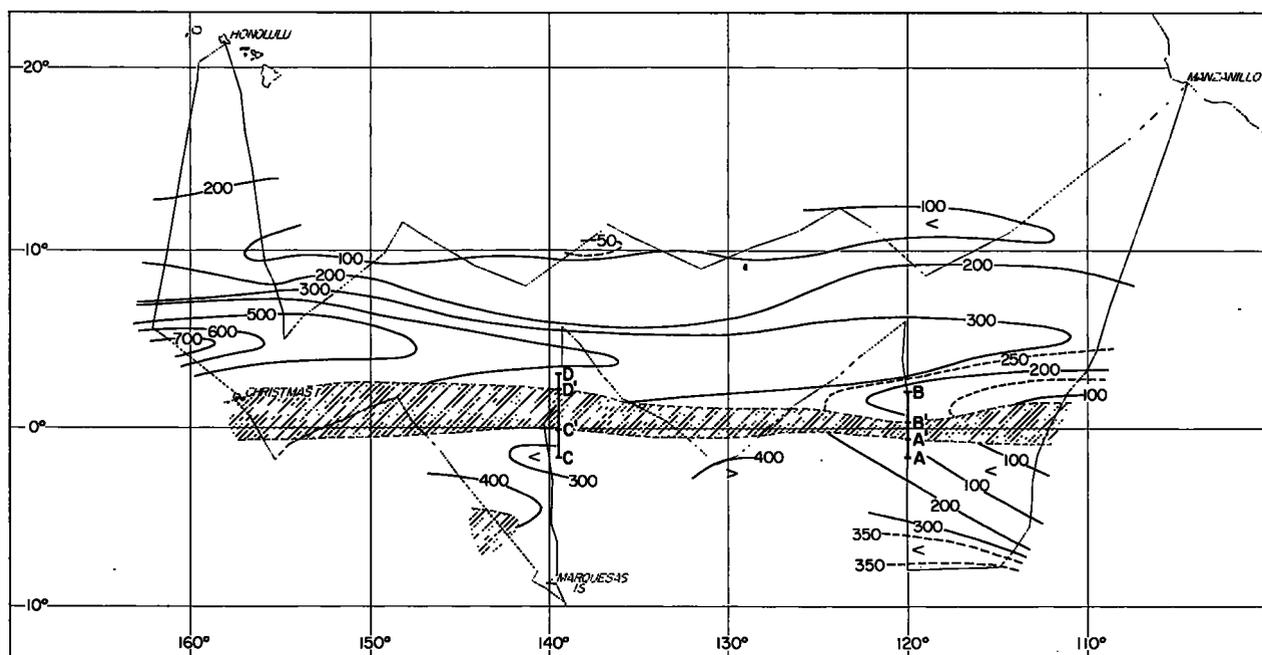


FIGURE 15.—Depth of the thermocline as determined from the BT data. (For explanation of shaded section, see text above.)

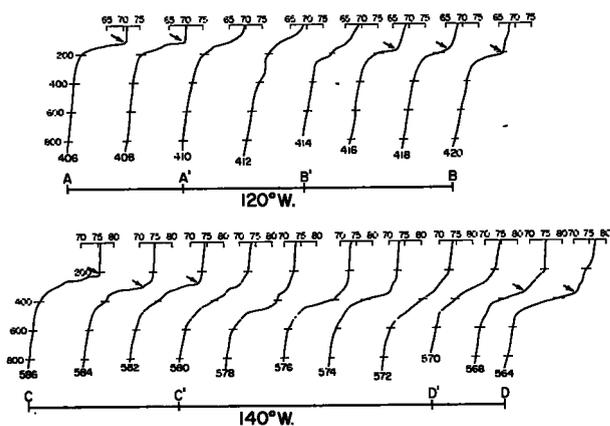


FIGURE 16.—Temperature–depth traces for selected BT records between A–B and C–D, figure 15. Arrows denote the thermocline depth as plotted in figure 15; the BT number is noted at bottom of each trace.

of the frontal line. Knauss (1957, table 1) reported a somewhat dissimilar situation, with higher salinities in the cooler surface waters to the south of the front (34.49 to 34.54) and a lower salinity to the north (34.46).

Phosphate

The concentration of inorganic phosphate (PO_4-P) in the surface waters was determined at

frequent intervals during the cruise. The results are shown in figure 18.

In the surface waters of the Countercurrent, the supply of this nutrient was relatively low. These are “old” waters in the classification of Steemann Nielsen (1954)—they have been at the surface for a considerable period of time as they have moved from the west in a current in which stabilization is markedly developed and vertical mixing is limited. East of 140° W., the surface values are below 0.5 $\mu\text{g. at./L.}$, a level regarded by Ketchum (1939) as limiting photosynthesis. These relatively low values (0.3 to 0.4 $\mu\text{g. at./L.}$) in the surface waters represent the balance in the mixed layer among utilization by the phytoplankton, biological regenerative processes, and vertical diffusion.

In the South Equatorial Current, the phosphate concentrations generally peak at or near the Equator with values of 1.0 $\mu\text{g. at./L.}$ or more. The concentrations decrease rapidly to the north and south, and more gradually east to west. Along 110° W. the highest concentration of phosphate was south of the Equator, peaking at about 4° S. This results from the proximity of the thermocline to the surface and wind mixing discussed in the section on surface temperature. The con-

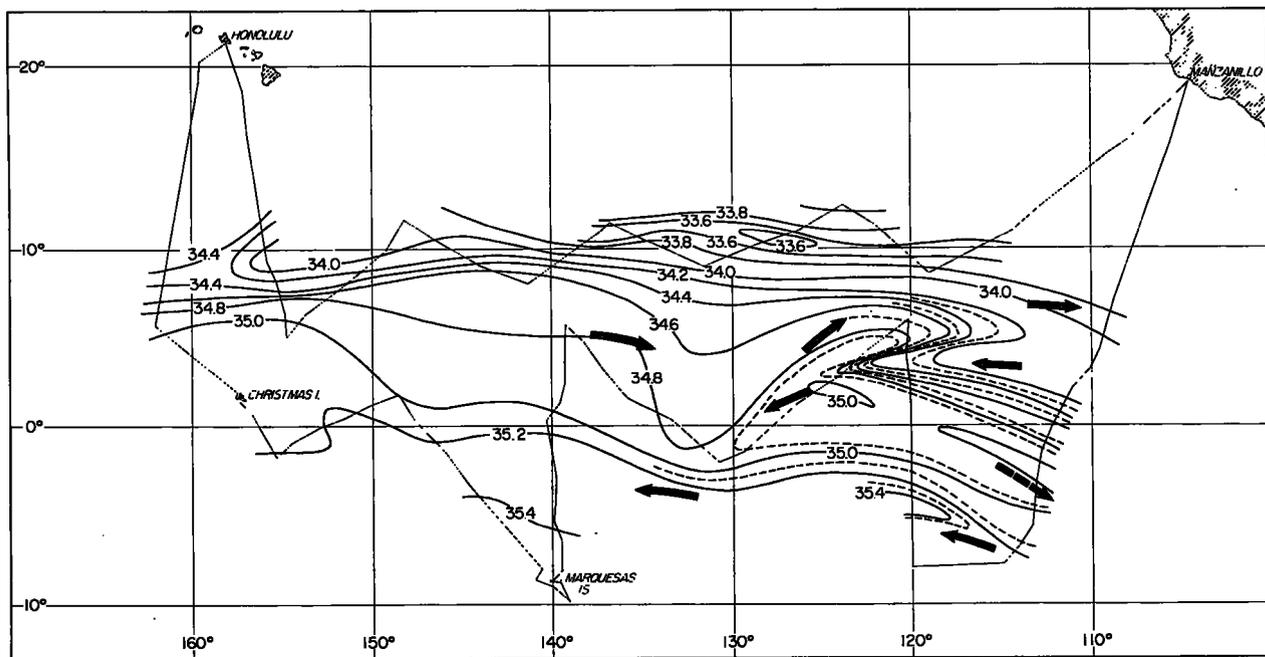


FIGURE 17.—Surface salinity (‰) distribution. The arrows denote current direction as determined from geostrophic calculations.

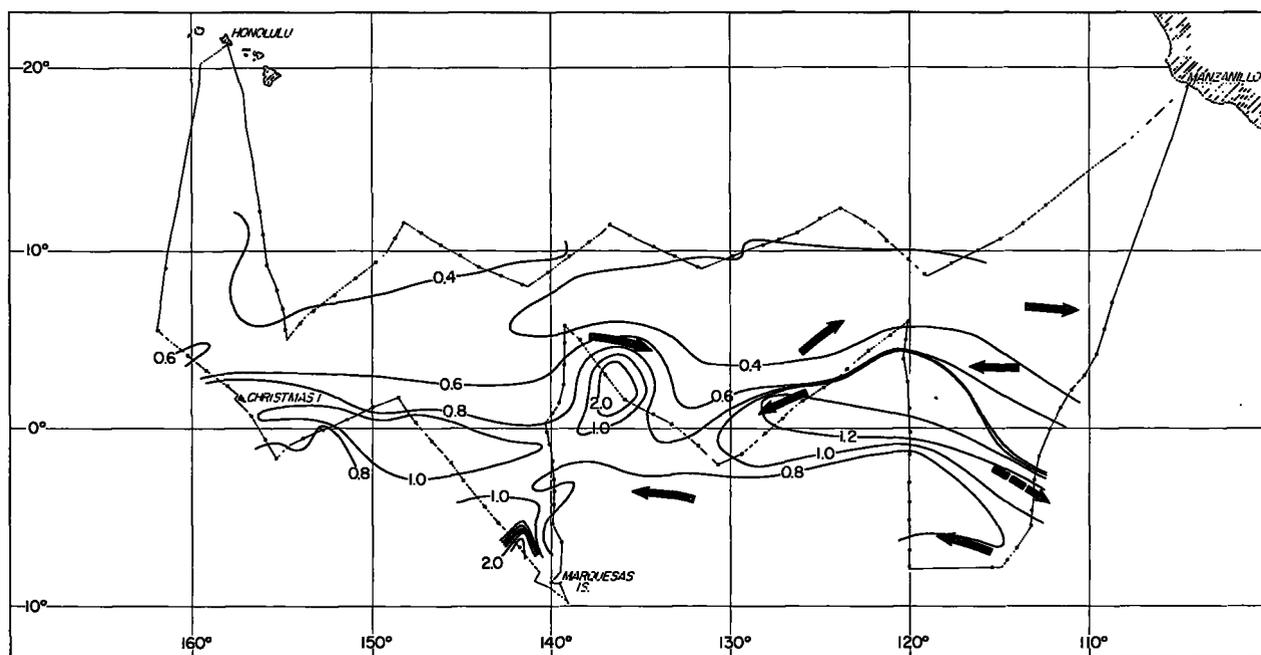


FIGURE 18.—Distribution of inorganic phosphate ($\mu\text{g. at./L.}$) in surface waters. Surface samples were taken at the position of the oceanographic stations and at the time of the BT lowerings. The positions at which the samples were taken are indicated. The arrows denote current direction as determined from geostrophic calculations.

centrations of 1.0 to 2.0 $\mu\text{g. at./L.}$ near 137° W. and 3° N. are difficult to explain. Unfortunately, there are no subsurface phosphates available for analysis of vertical transport, and no indications of such in the temperature fields. There are no apparent indications of analytical error. More than one sample is involved and the high values are consistent among these samples. One explanation is that these waters reached the surface near the Equator and moved to the position where sampled from the *Smith*. A similar situation was described by Sette et al. (1954) near 3° N. and 165° W. The high value near the Marquesas, 7° S., 142° W., may have resulted from some as yet undetermined circulation feature(s) associated with the islands. Similar concentrations in this area were observed during the recent participation of the *Smith* in Equapac (Austin 1957).

DISCUSSION OF RESULTS

Eastropic was a combined physical and biological study of the eastern central equatorial Pacific. The results of POFT's oceanographic observations have been described in the preceding sections of this report. The results of the biological sampling program will be considered in relation to

these environmental features. Before this can be done we must consider the question, "How typical were the environmental factors?" It appears that the oceanographic conditions were somewhat atypical.

The surface temperatures along the Equator (fig. 14) were 2°–4° F. cooler than normal; those in the Countercurrent showed little variation from normal. Waters were also cooler than normal at four stations in the eastern Pacific (fig. 19) one each off California, Panama, Peru, and Christmas Island (Line Islands group). Rodewald (1956) demonstrates that these below-normal surface temperatures were typical for the entire eastern Pacific during 1955, particularly the latter half of the year. North to south, he reports anomalies in 1955 of -0.9°F. for Alaskan waters, -1.7°F. for Washington and Oregon, -1.2°F. for California, and -0.6°F. for Chile and Peru. These temperatures and the cooler water observed by the *Smith* in the South Equatorial Current may be considered to be "eastern Pacific temperatures," while the normal temperatures in the easterly flowing Countercurrent more or less reflect conditions farther to the west. In the western Pacific near the Philippines, the anomaly in 1955

was $+0.2^{\circ}$ F., exceeding $+1^{\circ}$ F. for August through November.

The comparatively high measured and calculated speeds of surface flow in the South Equatorial Current, as well as the cooler than normal waters at the surface in the eastern Pacific, suggest that the circulation during expedition Eastropic was more vigorous than normally observed. If such was the case, this should be reflected in the distribution of mass.

Montgomery and Palmén (1940), using data from one station near $99^{\circ}07'$ W. and the mean of three near 135° E., calculated the mean slope of the sea surface (0/400 db. reference level) to be 4.0×10^{-8} , with a difference in level of 0.7 dynamic meter. In figure 20, using data from more recent cruises, the longitudinal variations in level of the sea surface over the 400-db. level are shown for the span between 100° W. and 140° E. longitude. Data from stations between $00^{\circ}30'$ N. and $00^{\circ}30'$ S. were used. The 400-db. level was chosen in order to increase the number of available stations. The slope from Montgomery and Palmén's report is also shown.

Of particular interest to this discussion is the slope between 100° W. and 140° W. For comparative purposes, the data from *Smith* cruise 35 (August–October 1956) and cruise 38 (January–

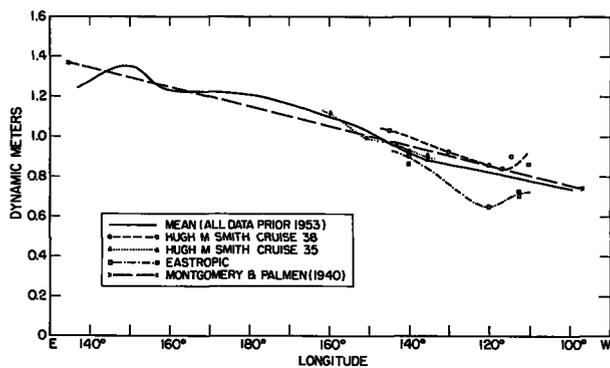


FIGURE 20.—Longitudinal slope, sea surface, 0/400 db. level.

March 1957) have been added. It may be seen that the slope during Eastropic was steeper than that for either of these two cruises or for the mean. Comparative values, 120° W. to 140° W., are: mean, 4.5×10^{-8} ; *Smith* cruise 38, 5.3×10^{-8} ; and Eastropic, 13.1×10^{-8} . A reversal in the calculated slope of the sea surface during Eastropic is evident near 120° W. (fig. 20). This reversal results from the deepening of the thermocline east of 130° – 120° W. (see fig. 5) and the accompanying increase in depth of the warmer, less-saline, and thus less-dense waters of the mixed layer.

The same features and conclusions can be inferred from the distribution of the depth of the 70° F. isotherm along the Equator (fig. 21). This isotherm is normally found near the center of the depth range of the thermocline (Austin 1954a), and thus exhibits the same variations in depth as the thermocline.

In figure 21, prepared from all available BT data from POFI files and those furnished by Scripps Institution of Oceanography, between 2° N. to 2° S., the variations in depth of the 70° F.

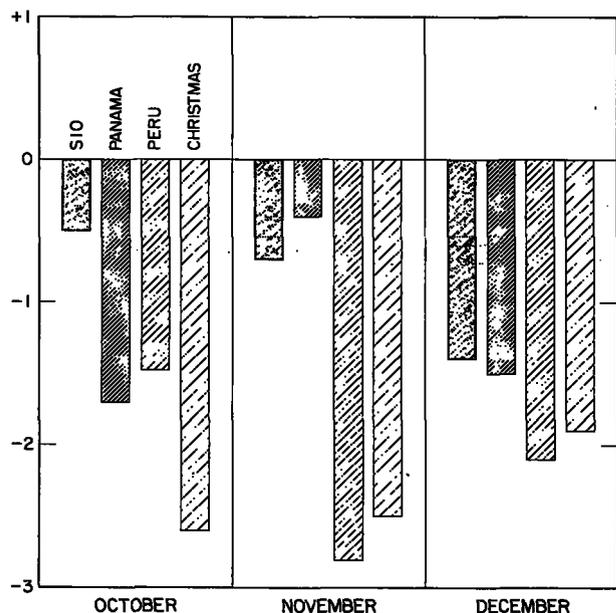


FIGURE 19.—Surface temperature anomalies ($^{\circ}$ F.) for four stations in the eastern Pacific for October, November, and December, 1955.

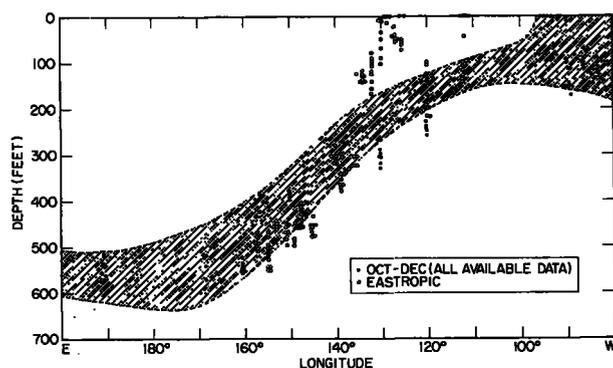


FIGURE 21.—Depth of 70° F. isotherm, 2° N. to 2° S.

isotherm, 80° W. to the 180th meridian are shown. The hatched "envelope" shows the approximate range of variation in depth among these data. Part of this variation results from seasonal fluctuations in the depth of the thermocline (Austin 1958), and part from the ridgelike configuration of the thermocline between 2° N. and 2° S. latitude. Data obtained prior to Eastropic for the months October through December (Eastropic cruise period) are shown by the solid dots and those during Eastropic by the small circles. Comparison of the mean (a curve through the center of the hatched band), the October-December data (dots), and Eastropic data (circles) demonstrates the comparatively steep slope of the thermocline during Eastropic. It is concluded that the comparatively steep slopes of the sea surface and the thermocline are associated with a more than normally active zonal circulation.

In the section describing the vertical distribution of temperature, we mentioned the 2-layer system which is typical of the tropics—the essentially homogeneous water from the surface down to the top of the thermocline, the thermocline (stable layer) through which the temperature decreases rapidly with increasing depth, and the extensive depth range below the thermocline to the ocean floor through which there is but a comparatively slight further decrease in temperature. This situation is typical of waters in the low latitudes throughout the seasons. In the middle and high latitudes, however, a deep mixed layer exists at the end of winter. As the season progresses, the depth of the mixed layer decreases to the mid-summer minimum and the depth of vertical turbulence is thus progressively restricted.

The development in the spring of the seasonal thermocline is termed "stabilization" by Sverdrup (1953, p. 291). He demonstrated that the onset of stabilization following the period of deep winter mixing played an important role in the vernal increase in biota. In the low latitudes, there is no such period of stabilization—the vertical density structure during all months is characterized by a mixed layer below which the density increases rapidly with depth and turbulence is suppressed. Therefore, when considering geographical and temporal variations in measurements of the biota in tropical oceans, we must look for mechanisms that will affect the degree of

stability or the depth of this stable layer in relation to the compensation depth. Within the area studied from the *Smith* during expedition Eastropic, we have mentioned several such mechanisms, including divergence of the surface waters and upwelling at or near the Equator, the effects of sheer and associated mixing at the boundaries of opposing currents, and the shallowing of the stable layer to a depth that will bring it within the euphotic zone, e.g., at the northern boundary of the Countercurrent. Although there may be seasonal variations, these mechanisms are all primarily related to horizontal and vertical transport features (as contrasted with the spring warming and stabilization and the fall cooling and overturn in the higher latitudes).

In higher latitudes, following stabilization, the nutrients in the mixed layer are quickly depleted by biological utilization and fallout of the organic material into or beneath the stable layer. Until the fall overturn and associated replenishment from below, the nutrient concentration in the mixed layer represents, primarily, a balance between utilization by the phytoplankton and the biological regenerative processes within this layer, with vertical diffusion playing a comparatively minor role. This situation characterizes vast areas of the tropical oceans during all months of the year. In figure 22, the vertical distribution of various properties is shown to illustrate conditions within the mixed, the stable, and the deeper layers at a position in the region of convergence north of the Equator (3° N.). It is to be noted that, at the particular station illustrated, within a very limited range of depth (≤ 50 meters), there is an abrupt change in the fields plotted. The temperature decreases nearly 10° C., the thermocline anomaly nearly 300 centiliters per ton (60 percent of total change, surface to 800 meters) and, of particular biological importance, the phosphate suddenly increases from 0.6 to 1.4 $\mu\text{g.at./L.}$ The other nonconservative property, oxygen, decreases from nearly 4 ml./L. to slightly less than 2.0 ml./L. within the same depth increment.

Nearer the Equator, however, the vertical distribution of properties differs somewhat from that shown in figure 22. In the discussion of the vertical distribution of oxygen, we described a feature with waters of comparatively high oxygen content that was positioned beneath the Equator. In each

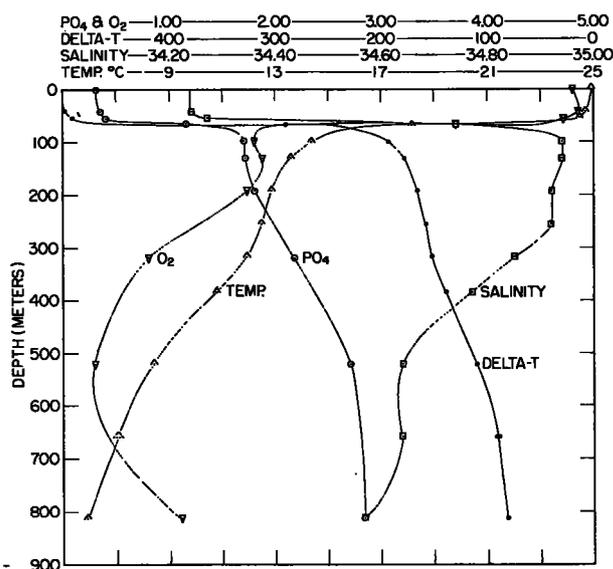


FIGURE 22.—Vertical distribution of temperature ($^{\circ}$ C.), density (cl./ton), oxygen (ml./L.), and phosphate (μ g.at./L.) from Hugh M. Smith station 4, $03^{\circ}13'$ N. latitude, $110^{\circ}12'$ W. longitude.

of the four sections shown in figure 11, this feature extended vertically from within or immediately below the thermocline to a maximum depth of between 300 and 400 meters and was approxi-

mately 200 miles wide. The oxygen content near its center was 2.8 to 3.0 ml./L. at 140° W., decreasing eastward to 2.5 to 2.7 near 100° W.

Consideration of the possible causes for this geographically restricted feature leads to the conclusion that it is the result of advection. In the first place, the deeper waters are essentially isolated from the oxygen-rich waters of the mixed layer above the thermocline. Even though isentropic principles may not apply near the Equator, the configuration of the density field shown in figure 10 suggests that there is little mixing between the waters in the surface layer and those beneath the thermocline. The oxygen content at depths between 100 and 300–400 meters decreases both to the north and to the south of the Equator.

To emphasize the meridionally limited extent of this feature, the distribution of oxygen on a surface of constant density (180 centiliters per ton) is shown in figure 23. In a narrow band along the Equator, between 140° W. and 120° W., the oxygen values are 3.0 ml./L. or greater. Between 120° W. and 110° W., the values decrease somewhat, then increase again farther to the east. If lateral mixing were significant across the Equator, the feature in question would be eliminated.

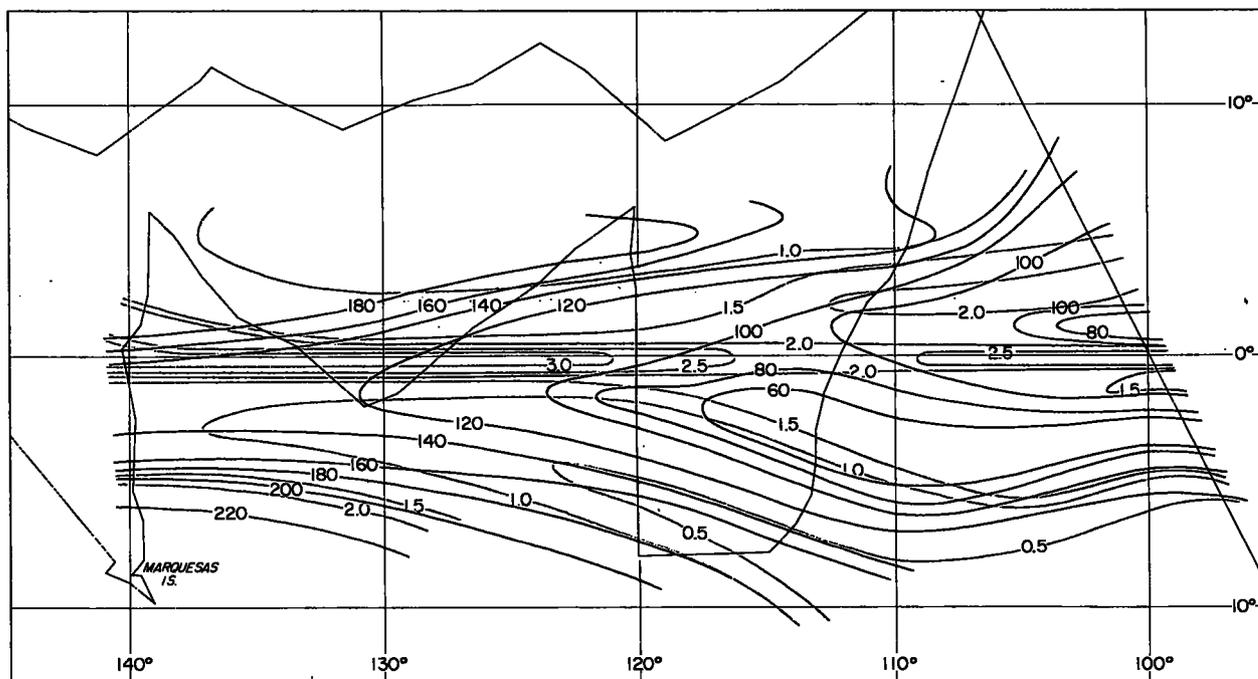


FIGURE 23.—Distribution of oxygen (ml./L.) in red on density surface (180 cl./ton) in black. Depth of density surface in meters.

From consideration of the standing crops of the biota in the euphotic zone near the Equator, oxygen values in the waters beneath the thermocline at the Equator should essentially be depleted and lower than to the north and south unless there was active replenishment. An inference to the standing crop of the phytoplankton may be made from the results of the use of the carbon isotope during expedition Eastropic (fig. 24). The highest rates of photosynthesis were at or very near the Equator where there is enrichment by upwelling (fig. 18). It is reasonable to assume that these higher rates of carbon fixation were associated with the larger standing crops of the phytoplankton. The different rates of photosynthesis among various species in, and the ages of, the populations (whether vigorously growing or senescent) are quantitatively unknown variables. King and Hida (1957, figs. 8 and 10) have shown that the standing crop of zooplankton reaches a maximum between approximately 1.5° N. and 1.5° S. latitude.

These facts and our present knowledge of the pattern of flow near the Equator lead to the conclusion that there is advection of waters with higher oxygen content from the west by the Equatorial Undercurrent. This subsurface, easterly directed flow was first reported by Cromwell, Montgomery, and Stroup (1954). They observed that the Undercurrent was both in the lower part

of the surface layer and in the upper part of the thermocline. Its total depth range, however, was not determined.

More recently, Knauss and King (1958), presenting preliminary results of a detailed survey of the Undercurrent made at 140° W. longitude, report that the vertical extent of the Undercurrent is between about 30 and 300 meters with the highest easterly velocities (2.0 to 3.5 knots) recorded at a depth of 100 meters. The Undercurrent was symmetrical about the Equator. At 2° N. and 2° S. latitude, the average thickness had decreased to 30 meters and the average maximum velocity to 0.6 knot. Of particular interest to the discussion of the results from expedition Eastropic, Knauss and King report that during the period of their cruise (March–June 1958), the Undercurrent showed no diminution in velocity between 140° W. and 92° W. and that the depth of its core rose from 100 meters at 140° W. to 42 meters at 98° W. Farther to the east, at 95° W. and 92° W., it once again deepened. At 89° W. the Undercurrent was missing.

In the section on vertical distribution of temperature (fig. 6), we discussed the configuration of the isotherms, particularly in the thermocline, as related to the Undercurrent. Between 2° N. and 2° S. there was a spreading of the isotherms, resulting in a shallow ridge and a deeper trough

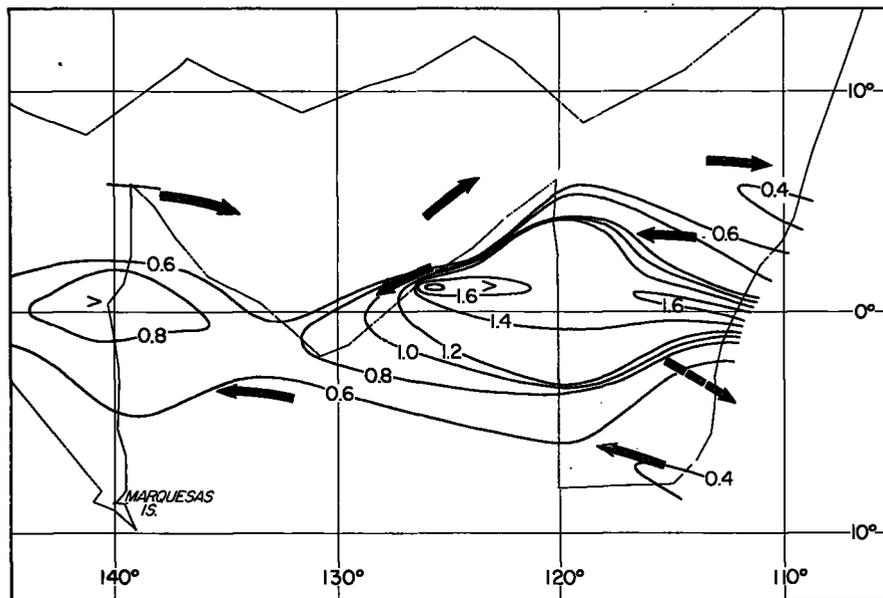


FIGURE 24.—Rate of carbon fixation (mg.C./hr./m.²) by photosynthesis as measured by uptake of the isotope carbon 14. (Data from King et al., 1957.)

about the Equator. This was interpreted as resulting from advection from the west of the somewhat warmer waters of the Undercurrent. Near the Equator, the thermocline shallowed between 160° W. and 120°–125° W. (fig. 5), then deepened once again. Considering these data and the results reported by Knauss and King (1958), it is assumed that, during Eastropic, the core of the Undercurrent exhibited a west-east variation in depth similar to that of the thermocline.

Oxygen and inorganic phosphate are both non-conservative (biologically affected) properties. Their concentrations normally exhibit reciprocal variations in the sea. This was the case in the waters beneath the Equator during Eastropic, at least along the 110° W. section (fig. 13), the only one for which adequate phosphate data are available. Between approximately 2° N. and 2° S., the meridional extent of the Undercurrent, the higher oxygen values previously discussed were accompanied by lower inorganic phosphate values, 1.6 $\mu\text{g.at./L.}$ or less as compared with 2.0 $\mu\text{g.at./L.}$ or greater at comparative depths to the north and south. Thus, the distribution of the two non-conservative properties and of temperature beneath the thermocline at the Equator is largely governed by the easterly flowing Undercurrent, while their distribution in the shallower portion of the thermocline and the mixed layer is largely related to upwelling.

There are various references to the oceanographic conditions along the northern boundary of the Countercurrent which use the words "divergence" or "upwelling." Relative measurements of the standing crops of the marine biota, especially zooplankton, have been used to support the hypothesis that divergence of the surface waters along this boundary has resulted in enrichment within the euphotic zone. Sverdrup et al. (1942, p. 711), suggest that a transverse circulation is superimposed on the flows to the east (the Countercurrent) and to the west (the North and South Equatorial Currents). Such a transverse circulation would require a divergence at the northern boundary of the Countercurrent and a convergence at the southern boundary. Referring to the relative volumes of the plankton samples taken aboard the *Carnegie* as reported by Graham (1941), they suggest that the relatively high

volume at *Carnegie* station 151 (13° N.) was associated with a divergence centered near 10° N. (Sverdrup et al., 1942, fig. 219). This biological evidence may be somewhat speculative as Graham (1941, p. 193) states that this sample (station 151) was "not quite comparable as it contained a large colony of salps." The sample (expressed as dry weight and not as volume) was not used by Graham in his analyses of plankton abundance along the *Carnegie's* transequatorial section (his fig. 41).

Jerlov (1956, p. 150), discussing the results of the *Albatross* expedition in the central equatorial Pacific, assumes from consideration of the relative distribution of particles that "there is ascending water movement along σ_t -surfaces which enriches the upper layer with nutrients." His figure 34 shows a maximum concentration of particles at the northern edge of the Countercurrent. Jerlov suggests that the distribution of these particles "largely represents phytoplankton population and plankton remnants, as the supply of terrigenous components in this area must be low."

Austin (1954a) does not recognize the presence of upwelling at the northern boundary of the Equatorial Countercurrent in the central Pacific, but does acknowledge the fact that the shallow thermocline in this area (see fig. 15, this report), coupled with wind mixing, may result in an increase in the biota. A question of semantics may be involved. Austin and Rinkel (in press) have defined upwelling as a local, wind-induced divergence of the surface waters resulting in a mixing of the deeper, cooler, nutrient-rich waters with those at the surface. Within the scope of this definition, there is no evidence of upwelling along the northern boundary of the Countercurrent in the Eastropic data. Although there was a marked ridge in the thermocline, there was no evident cooling of the surface waters (see fig. 14). At the northern edge of the Countercurrent any upwelling would result in a band of more-saline waters and waters with higher phosphate concentrations. Salinities were comparatively low, increasing to either side of the northern edge of the Countercurrent (fig. 17). Phosphate concentrations were low, averaging 0.4 $\mu\text{g. at./L.}$ or less, these to be compared to 0.8 to 1.0 $\mu\text{g. at./L.}$ near the Equator (fig. 25).

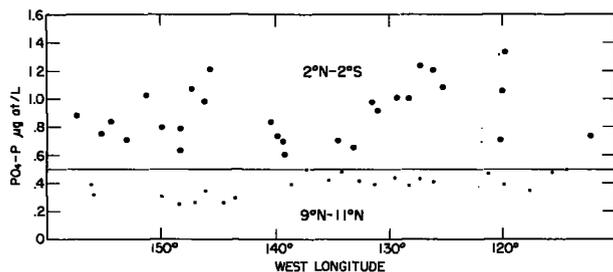


FIGURE 25.—East-west variations in surface inorganic phosphate concentrations ($\mu\text{g.at./L.}$) between 2° N. and 2° S. latitude and 9° N. and 11° N. latitude.

An important biological consideration is the fact that along the northern boundary of the Countercurrent the thermocline in the eastern Pacific is sufficiently shallow to be within the euphotic zone. If we assume that in these tropical waters seasonal variation in light is not a limiting factor, Sverdrup's concept of critical depth is applicable (Sverdrup 1953). With the thermocline penetrating into the euphotic zone (shallower than the compensation depth, ca. 100 meters), the phytoplankton in the mixed layer is retained within the depth range of active photosynthesis; i.e., not carried by vertical mixing to a depth during the day where respiration exceeds photosynthesis. To the north and south of the northern boundary of the Countercurrent, and west of about 150° W., the thermocline deepens and is normally deeper than the compensation depth.

Biological data from this area are pertinent. King and Hida (1957), discussing the results of POFI's zooplankton program in the central equatorial Pacific, 1951 to 1954, show that zooplankton volumes in the Countercurrent are comparatively low, 180° meridian to 150° W. longitude (ca. 25 cc./1000 m.³) but increase to nearly 45 cc./1000 m.³ between 140° W. and 120° W., a volume approximately equal to that of the region of the divergence near the Equator. They also demonstrate (fig. 11) that, between 8° N. and 11° N., the plankton volumes increase west to east (170° W. to 140° W.) as the depth of the thermocline decreases. Thus, the available empirical data suggest that any relative increase in the standing crops of the biota along the northern boundary of the Countercurrent is more directly related to the presence of a shallow thermocline than to a divergence and upwelling in the surface waters.

SUMMARY

A cooperative oceanographic survey of the central and eastern tropical Pacific (expedition Eastropic) was conducted during the period September–December 1955, with five research vessels participating, representing five agencies: Scripps Institution of Oceanography, Inter-American Tropical Tuna Commission, California Department of Fish and Game, Pacific Oceanic Fishery Investigations (POFI) of the U. S. Fish and Wildlife Service, and the Peruvian Navy.

As POFI's participation in Eastropic, the *Hugh M. Smith* (cruise 31) completed an 86-day, 14,000-mile cruise, obtaining information on east-west gradients in temperature, salinity, phosphate, zooplankton, and forage fish abundance along the northern boundary of the Equatorial Countercurrent and along the Equator between 110° W. and 156° W. longitude. A survey of tuna bait-fish was conducted in the Marquesas Islands and, in collaboration with the University of Hawaii, carbon fixation and chlorophyll measurements were made on the westbound leg of the cruise.

Sea surface temperatures along the Equator were from 2° to 4° F. cooler than normal; those in the Equatorial Countercurrent deviated little from normal. Temperature anomalies for the eastern Pacific, Alaskan waters south to Peru, were generally negative (-0.6° F. to -2.0° F.) for the latter half of 1955.

Near the Equator, the observed east-west slope of the thermocline was considerably steeper than normal, shallowing from near 500 feet beneath the surface at 160° W. longitude to at or near the surface at 125° W., then deepening somewhat to the east.

A pronounced oceanic temperature front, across which there was a temperature change of approximately 3° F., was observed near 4° N., 120° W. The same or a similar feature was observed (1 month later) from the Scripps Institution of Oceanography vessel, the *Horizon*, near 3° N., 120° W.

Calculated current velocities in the warmer waters to the north of the front were westerly, 1.8 to 2.3 knots, decreasing to 0.2-knot westerly flow in the cooler water to the south of the front. In the eastern portion of the area surveyed from the *Smith* (Equator to 4° N., 120° W.), velocities

measured from Scripps vessels were as high as 2.0 knots (324° T., measured at 3°08' N. near 120° W.).

The calculated east-west slope of the sea surface (0/400-db. level) was greater than the mean; 0.66 dynamic meters at 120° W. (mean=0.85) sloping upward to 0.90 dynamic meters near 140° W. (mean=0.92) for a difference of 0.24 dynamic meter as compared with 0.07 for the mean.

Upwelling and wind mixing, coupled with a shallow thermocline, resulted in considerable enrichment of the surface waters along the Equator. Concentrations of inorganic phosphate at the surface were between 0.8 and 1.2 $\mu\text{g. at./L.}$ in the region of the shallow thermocline (near the Equator and 125° W. and near 4° S. and 115° W.). Phosphate concentrations in the surface waters of the Countercurrent and along the northern edge of the Countercurrent were uniformly low, $\leq 0.4 \mu\text{g. at./L.}$

Cooler than normal surface temperatures, comparatively steep east-west slopes in the sea surface and the thermocline, comparatively high calculated and measured current velocities, and high inorganic phosphate concentrations in the surface layer, all suggest the horizontal and vertical circulation features, 5° N. to 5° S. along the Equator, were more dynamic during Eastropic than normally observed.

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DEFINITION OF HADDOCK STOCKS OF THE NORTHWESTERN ATLANTIC

BY JOHN R. CLARK AND VADIM D. VLADYKOV



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ABSTRACT

Differences in average vertebral number, related to temperature on the spawning grounds, have been used to separate northwestern Atlantic haddock into five major stocks: Newfoundland, eastern Nova Scotian, central Nova Scotian, western Nova Scotian, and New England.

DEFINITION OF HADDOCK STOCKS OF THE NORTHWESTERN ATLANTIC

By JOHN R. CLARK, *Fishery Research Biologist*, and VADIM D. VLADYKOV, *Fishery Biologist*

Haddock are distributed over the continental shelves of the North Atlantic Ocean and in no other waters. They are not distributed continuously over this vast range, but reside in certain areas delimited by topographic and hydrographic boundaries. Nor are they evenly distributed within any area. Haddock generally prefer depths of less than 110 fathoms. They are presently considered to belong to a single species, *Melanogrammus aeglefinus* (L.).

In the northwestern Atlantic, haddock appear on certain fishing grounds only during the winter or spring for spawning. Some grounds support fisheries for haddock only during the summer and autumn while others are fished throughout the year. The character of populations sustaining year-round fisheries often varies from season to season, with older fish appearing for spawning and younger fish replacing them during the remainder of the year.

Age composition, growth rate, and other characteristics of haddock population units differ from place to place, causing us to believe that the species consists of many more-or-less separate units. This idea is strengthened by tagging experiments in the western Atlantic which have shown that haddock, although migrating over rather definite routes, infrequently cross the deep-water channels separating the New England, Nova Scotian, and Newfoundland Banks (fig. 1). On the basis of such evidence, Needler (1930) suggested a subdivision of northwestern Atlantic haddock into three major units: the New England, Nova Scotian, and Newfoundland stocks. Further research has, in general, substantiated this division (Schroeder 1942; Schuck and Arnold, 1951; Vladykov 1935). Each of the three regions

encompasses a number of distinct grounds which support important fisheries at various times of the year.

Properties of the environment, notably temperature, differ from one fishing ground to another. These properties may be expected to significantly modify the meristic characters of haddock as they do of other species. Notwithstanding the effect of genetic influences, the differences in these characters should permit identification of broods originating in different localities. It is the purpose of this paper to demonstrate that one meristic character, the number of vertebrae, can be used to identify haddock stocks.

COLLECTION OF DATA

Our collection of vertebral counts was begun in 1932, and a preliminary study was published (Vladykov 1935) which demonstrated recognizable differences for the haddock of various western Atlantic fishing grounds. Since then the Fisheries Research Board of Canada and the U.S. Fish and Wildlife Service have added many thousands of counts to the collection, representing altogether the haddock of 16 major fishing grounds from New England to Newfoundland. The samples have come from the catches of commercial fishermen and research vessels using otter trawl and hook-and-line gear.

The entire collection of data is detailed in table A-1 of the Appendix, p. 294. In counting the vertebrae, all of them from the first vertebra, found immediately behind the basi-occipital bone, to the penultimate one, which has a normal centrum and a hypural plate, are included. The last vertebra with its modified centrum and terminal hypural plate is not included in our counts. Fish having vertebral abnormalities, such as fused centra, amounted to slightly more than 1 percent of the total number of specimens and were not used.

NOTE.—John R. Clark, North Atlantic Fishery Investigations, U.S. Bureau of Commercial Fisheries; Vadim D. Vladykov, Department of Biology, University of Ottawa, Ottawa, Ontario. Approved for publication, April 10, 1959. Fishery Bulletin 169.

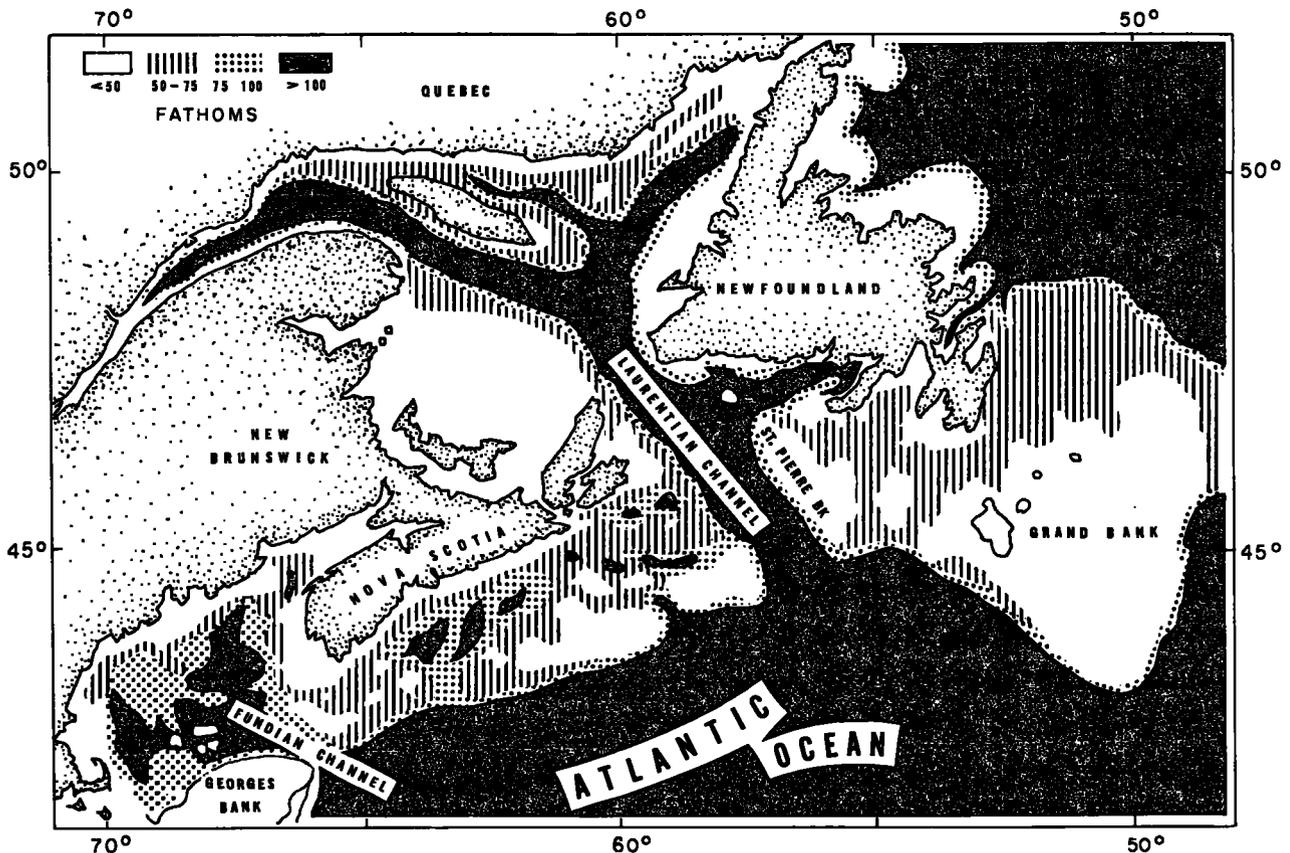


FIGURE 1.—The submarine physiography of the Continental Shelf from Labrador to Cape Cod. (Adapted from Hachey, Hermann, and Bailey, 1954.)

GEOGRAPHICAL VARIATION IN VERTEBRAL NUMBERS

In studies of many species, the number of vertebrae has been shown to differ significantly among geographically separated units of the population. The number of vertebrae typically increases with latitude, suggesting an inverse relation with water temperature.¹

To investigate the possibility of such a relation between number of vertebrae and water temperature for haddock, we grouped our samples by fishing ground and calculated the average number of vertebrae for each (appendix table A-2). A difference of nearly 1.3 vertebrae is shown between the highest and lowest averages. Analysis-of-

variance treatment of the data (see appendix) showed these differences between the grounds to be highly significant ($F = 182$).

As shown in figure 2, the number of vertebrae tends to increase from Georges Bank northeasterly along the Scotian Shelf. The average for St. Pierre Bank, however, is lower than even the one for Georges Bank.

Another presentation of these data is given in figure 3 where we have plotted, after the method of Hubbs and Perlmutter (1942), the main statistical values for the data from each fishing ground: total range of items, standard deviation, mean, and two standard errors either side of the mean. Here we see that numbers of vertebrae increase regularly from Georges Bank to Emerald Bank, hold relatively constant from Emerald Bank to the Gulf of St. Lawrence, then drop sharply to St. Pierre Bank. The significance of these differences is shown by comparison of the standard errors of the various distributions.

¹ See, for example, Schmidt 1930, Thompson 1943, Hansen 1949, for cod; Bertelsen 1942, for coalfish; Täning 1929, Devold 1942, for plaice; Runnström 1941, Tester 1949, McHugh 1954, for herring; Hansen 1943, Templeman 1948, for capelin; Clark 1947, for sardine; Hubbs and Perlmutter, 1942, McHugh 1951, for anchovy; Vladykov 1934, for summary of earlier information.

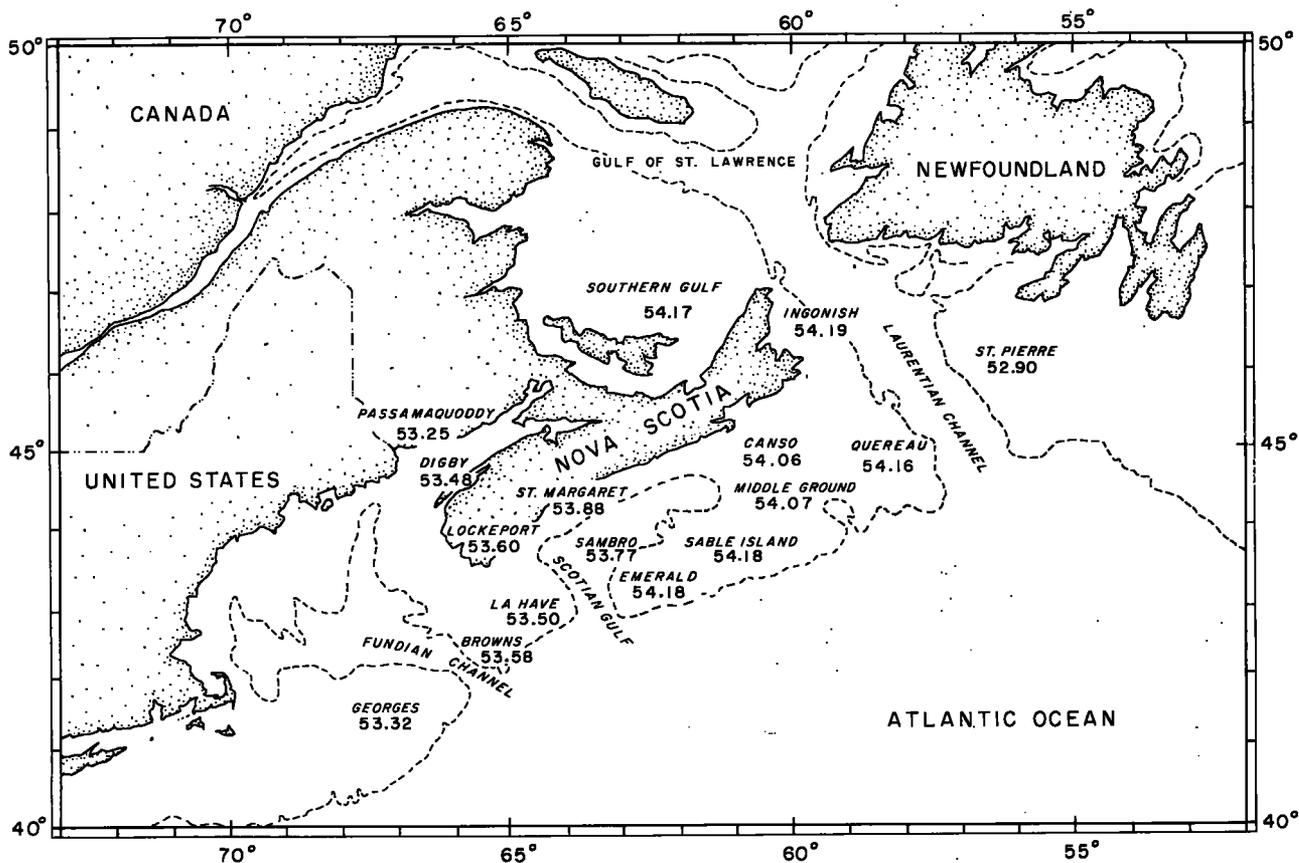


FIGURE 2.—Haddock fishing grounds of the northwestern Atlantic and the mean number of vertebrae of haddock from each.

VERTEBRAL NUMBERS AND WATER TEMPERATURE

Since water temperatures decrease from Georges Bank northeasterly along the coast, we see that haddock conform in general to the typical negative relation of meristic characters and temperatures. To discover how close this correspondence is, we must examine the temperature regime on each fishing ground during the time when the number of vertebrae is actually established.

It is probable that vertebral numbers are established within the first week or so following fertilization of the eggs. We do know for certain that all myomeres are formed by the time the fish reaches 13 mm. in length, which requires 5 or 6 weeks. Although haddock spawn on or near the bottom, their eggs are buoyant and rise toward the surface following fertilization.² Since the

eggs tend to be concentrated near the surface, the temperatures of the surface layer are most appropriate. We have, therefore, gathered such information as is available on surface water temperatures during the spawning period of northwestern Atlantic haddock to compare with their average numbers of vertebrae.

Haddock spawn in greatest numbers in mid-March in the New England area, in late March and early April in the Nova Scotian area, and in late May and June in the Newfoundland area.³ Unpublished surface temperature records representing all available observations during these spawning times were obtained from the Woods Hole Oceanographic Institution. These data are plotted as isothermic lines in figure 4. The temperature for each fishing ground has been estimated from the chart and listed along with the

² See Walford (1938) for a discussion of the distribution and development of the early stages of northwestern Atlantic haddock.

³ Needler 1930; Vladykov and Homans, 1935; Bigelow and Schroeder, 1953; Thompson 1939; and unpublished records of the U.S. Fish and Wildlife Service.

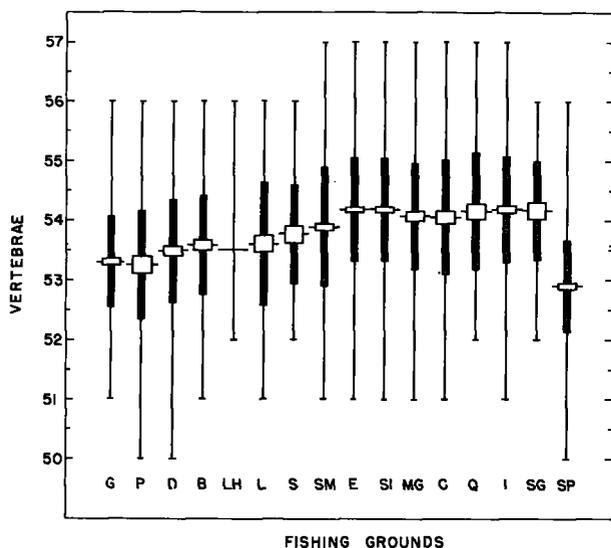


FIGURE 3.—Numbers of vertebrae of haddock from fishing grounds of the northwestern Atlantic. The vertical line represents the range; the solid bar, one standard deviation on each side of the mean; the hollow rectangle, two standard errors on each side of the mean; and the crossbar, the mean. The fishing grounds shown are Georges Bank (G); Passamaquoddy Bay (P); Digby (D); Browns Bank (B); La Have Bank (LH); Lockeport (L); Sambro Bank (S); St. Margaret's Bay (SM); Emerald Bank (E); Sable Island Bank (SI); Middle Ground (MG); Canso Bank (C); Quereau Bank (Q); Ingonish (I); Southern Gulf of St. Lawrence (SG); St. Pierre Bank (SP).

appropriate spawning time in table 1. A negative relation between temperature and vertebral number is demonstrated by the data. The apparent anomaly for St. Pierre Bank is now easily explained by the high water temperature obtaining there during the spawning time (May-June).

TABLE 1.—Mean number of vertebrae and average surface water temperature during spawning time for haddock of the northwestern Atlantic

Fishing ground	Temperature (° F.)	Mean number of vertebrae
St. Pierre Bank.....	43.5	52.90
Georges Bank.....	38.0	53.32
Digby.....	37.0	53.43
Passamaquoddy Bay.....	36.5	53.25
Browns Bank.....	36.5	53.58
La Have Bank.....	36.0	53.50
Emerald Bank.....	36.0	54.18
Lockeport.....	35.5	53.60
Sambro Bank.....	35.0	53.77
Sable Island Bank.....	34.5	54.18
St. Margaret's Bay.....	34.0	53.88
Middle Ground.....	34.0	54.07
Canso Bank.....	33.5	54.06
Quereau Bank.....	33.0	54.16
Ingonish.....	32.0	54.19
Southern Gulf of St. Lawrence.....	32.0	54.17

Some data are available for the northeastern Atlantic for comparison with northwestern Atlantic data. Tåning (1935) listed average numbers of vertebrae that show little relation to latitude in the North Sea, Ireland, Iceland, Faroes, and Norway. Nor could Saetersdal (1952) find a relation in his data between latitude and vertebral numbers along the Norwegian coast. However, upon treating spawning-time temperatures and vertebral averages for these northeastern Atlantic data in the manner described previously for our data,⁴ we find evidences of a relation between the two (table 2 and fig. 5).

TABLE 2.—Mean number of vertebrae and average water temperature during spawning time for haddock of the northeastern Atlantic

Area ¹	Temperature (° F.)	Mean number of vertebrae ²
Ireland.....	47.5	52.84
Faroe Islands.....	45.0	52.88
Iceland.....	44.0	52.96
North Sea.....	43.0	53.04
Norway.....	41.0	53.12
Norway ³	41.0	53.03

¹ From Tåning (1935).

² A single average was calculated where ranges were given or more than one mean was presented in the original publication.

³ From Saetersdal (1952).

The average vertebral numbers for haddock from both sides of the Atlantic have been plotted against surface water temperatures at spawning time and a curve has been fitted to them (fig. 6). The data thus assembled include the entire known range of spawning-time temperatures of haddock.

A similar relation between average number of vertebrae and temperatures at spawning time is shown for both sides of the Atlantic. This, together with the overlapping range in vertebral numbers of the Newfoundland and northeastern Atlantic samples, suggests that a single vertebral number-temperature relationship applies to the species throughout its range. Temperature would then appear to be an important factor in the variation in number of vertebrae of haddock.

⁴ Data on spawning times of northeastern Atlantic haddock have come from Schmidt 1909, Wiborg 1950, Thompson 1928, and Raitt 1948. These data indicate that haddock spawn in greatest numbers off Norway and in the North Sea in late March, off Iceland and Ireland in mid-April, and off the Faroe Islands in early May. Temperature data are from Conseil Permanent International pour l'Exploration de la Mer, (1933) and U.S. Hydrographic office (1944).

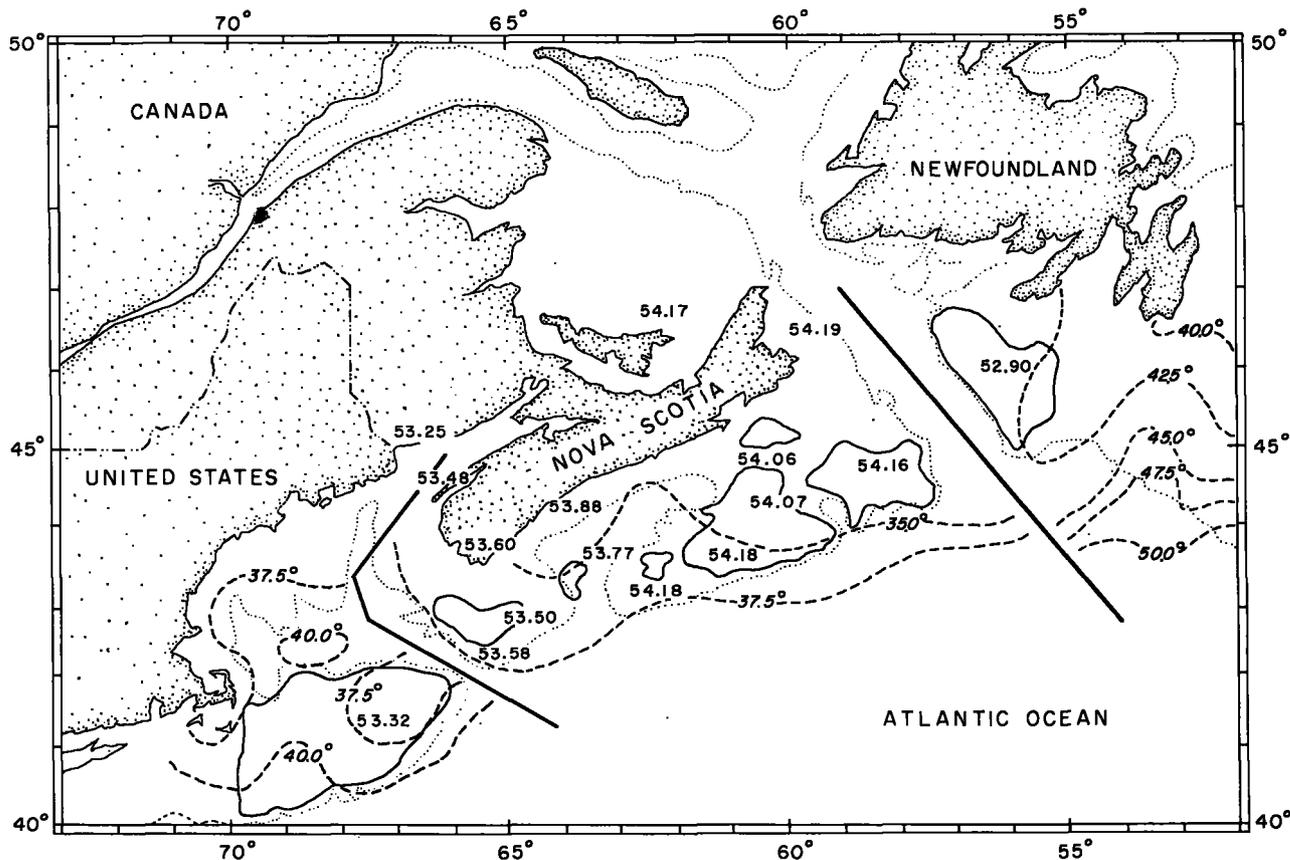


FIGURE 4.—Mean numbers of vertebrae of haddock from fishing grounds of the northwestern Atlantic and surface water temperatures ($^{\circ}$ F.) during spawning time.

VERTEBRAL NUMBERS AND YEARLY VARIATIONS IN WATER TEMPERATURE

The evidence presented suggests that annual variations in water temperature in any particular locality would cause haddock originating in that locality to have varying numbers of vertebrae. Temperature at time of spawning and average number of vertebrae for individual year classes have been successfully correlated for herring by McHugh (1942), Rounsefell and Dahlgren (1932), and Tester (1937, 1938, and 1949).

Data are not available with which to assign ages to most of our specimens, and the year classes must for the most part be treated together. Some material, however, was available to evaluate differences among certain year classes on Georges and Browns Banks. This material was collected during two trips of the *Albatross III* in the spring and autumn of 1950. We obtained 369 specimens from Browns Bank and 974 specimens

from Georges Bank which were taken over widely separated areas of each bank and so adequately represented the population present at the time. The ages of the fish were determined from their scales. The vertebral numbers are given in table 3 for each year class. Since the reliability of age determination from scales is uncertain for haddock over 8 years of age, we have grouped the older fish into a single category (9+) and have not assigned them to year classes.

Analysis-of-variance treatment of the data showed the difference between average vertebral numbers from the two banks to be highly significant ($F=10.51$).

The difference between year classes is highly significant only for Georges Bank ($F=4.63$). Although the Browns Bank year classes are not shown by analysis of variance to differ significantly ($F=1.82$), we have used them since the magnitude of the differences was even greater than for Georges Bank.

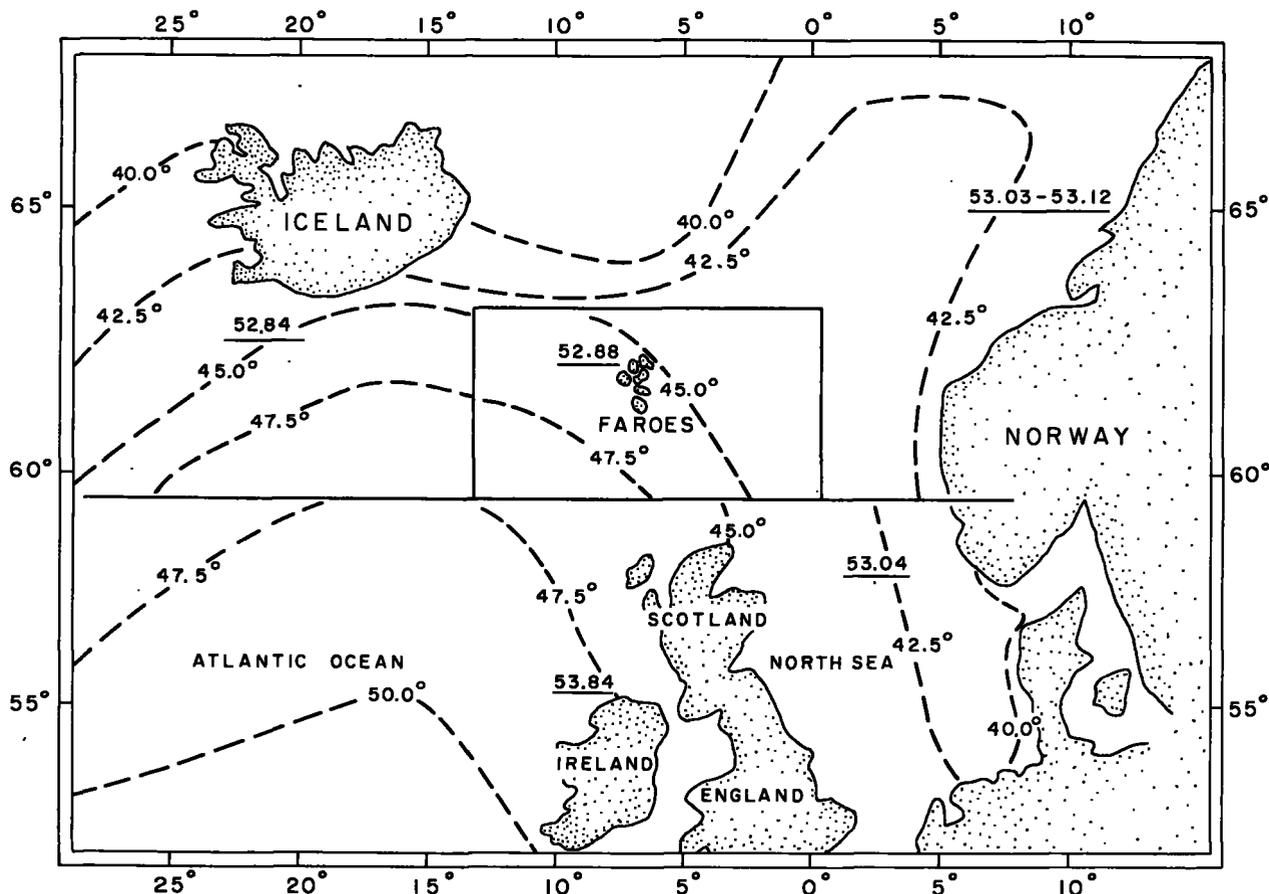


FIGURE 5.—Mean numbers of vertebrae of haddock from the northeastern Atlantic and temperatures ($^{\circ}$ F.) during spawning time.

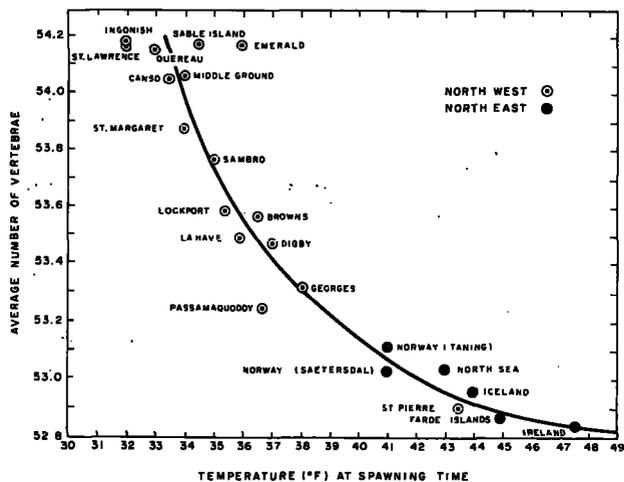


FIGURE 6.—The relation between water temperature during spawning time and numbers of vertebrae of haddock.

No series of temperature observations is available directly from Browns and Georges Banks for the period 1942-49 to use in correlating with ver-

tebral averages of the year classes. A continuous series of records is available (U.S. Coast and Geodetic Survey, 1947), however, for surface water temperatures at Eastport, Maine, in Passamaquoddy Bay, near the entrance to the Bay of Fundy. Hachey and McLellan (1948) have demonstrated that temperatures for Passamaquoddy Bay give a reliable measure of annual temperature variation along the northwestern Atlantic coast.

To utilize these data from Eastport, Maine, we found it necessary to relate them to the temperatures on the two banks for individual years. The average surface water temperature over Browns Bank during the time of haddock spawning is shown in table 1 to be about 36.5° F., and the average water temperatures at Eastport for the same period of the year are shown in table 4 to be the same. The average surface temperature during the spawning time on Georges Bank, how-

TABLE 3.—Vertebral-number frequencies for each age of haddock from Georges and Browns Banks

Age (years)	Year class	Georges Bank							Browns Bank									
		Number of fish	Occurrence of vertebrae numbering—						Mean	Number of fish	Occurrence of vertebrae numbering—						Mean	
			50	51	52	53	54	55			56	50	51	52	53	54		55
1.....	1949	32			5	17	8	2	53.22	1				1				
2.....	1948	381		1	24	153	173	30	53.54	41			3	18	19	1		53.44
3.....	1947	76	1		10	42	22	1	53.14	76		1	6	31	32	6		53.47
4.....	1946	137	1	1	19	59	44	13	53.34	100		1	6	35	48	9	1	53.61
5.....	1945	194		5	25	95	60	9	53.22	60		1	5	29	19	6		53.40
6.....	1944	82		2	6	40	26	7	53.40	50			4	15	24	7		53.68
7.....	1943	39			3	19	13	3	53.49	30			1	11	11	6	1	53.83
8.....	1942	15			1	10	3	1	53.27	4				3				
9+		18			2	5	10	1		7		1		3	1	2		
All ages.....		974	2	9	95	440	359	67	53.39	369		4	25	145	156	37	2	53.55

ever, approximates 38° F. while temperatures at Eastport for the same period average 35.6° F. Temperatures on Browns Bank can therefore be estimated directly from readings at Eastport, but estimates for Georges Bank require an adjustment of about 2.5° F.

An average of the April readings for Eastport was, therefore, used to approximate spawning time temperatures on Browns Bank. The March-April average for Eastport was increased by 2.5° F. to estimate spawning time temperatures for Georges Bank.

The temperature estimates thus obtained are listed for the years 1942 to 1949 in table 4, along with the average number of vertebrae for the haddock spawned in those years. The 1942 and 1949 year classes for Browns Bank are represented by too few specimens to give meaningful results and have not been included. These data indicate a close correlation between water temperature and number of vertebrae of the year

classes. How this compares with the previous relationship (fig. 6) can be seen in figure 7, where we have imposed the temperature-vertebrae data for our year classes from Browns and Georges Banks over the curve from figure 6. The curve fitted to the data from the Georges and Browns year classes deviates very little from the curve representing all the fishing grounds.

TABLE 4.—Estimated surface water temperature at spawning time and mean number of vertebrae for certain year classes of haddock from Georges and Browns Banks

Year class	Georges Bank			Browns Bank	
	March-April mean temperature at Eastport (°F.)	Adjusted mean temperature (°F.) ¹	Average number of vertebrae	April mean temperature at Eastport (°F.)	Average number of vertebrae
1949.....	37.4	39.9	53.22		
1947.....	37.2	39.7	53.14	39.0	53.47
1945.....	37.0	39.5	53.22	37.9	53.40
1946.....	35.8	38.3	53.34	37.2	53.61
1942.....	35.4	37.9	53.27		
1948.....	34.8	37.3	53.54	35.8	53.44
1944.....	34.4	36.9	53.40	35.6	53.68
1943.....	33.0	35.5	53.49	34.3	53.83
Mean.....	35.6			35.5	

¹ See text for explanation.

IDENTIFICATION OF POPULATION UNITS

It appears from the consistency of the vertebral number-temperature relation that we should be able to predict, within limits, the average number of vertebrae of haddock from any area if we know the temperature at spawning time. The deviations from the curve in figure 6 may represent fish not spawned on the grounds where they were captured. In like manner, the points falling near the line may represent stocks which were spawned on the grounds where captured or on

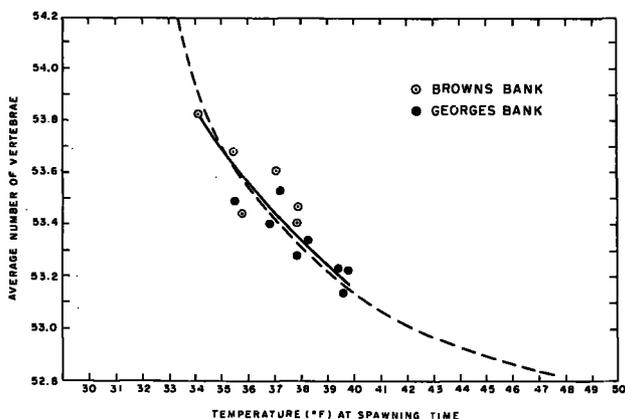


FIGURE 7.—The vertebrae-temperature relation for individual year classes from Georges and Browns Banks. (Dashed line from fig. 6.)

grounds having similar temperatures at spawning. Some interesting points may be brought forth by considering the data for each fishing ground with these suggestions as an hypothesis:

St. Pierre Bank.—The data fit closely to the curve, indicating negligible movement of other haddock to this area.

Georges Bank.—Following the same reasoning as for St. Pierre, Georges Bank haddock appear to reside in the area of their origin with no significant immigration.

Passamaquoddy Bay.—Haddock are known to be summer visitants only to this area, with spawning taking place elsewhere. Their average vertebral number indicates that they are probably hatched in waters having temperatures higher than 38° F. As water of this temperature is usually found in the western Atlantic only in the vicinity of Georges Bank during the spawning time of haddock (see fig. 4), we may assume that the Passamaquoddy haddock were spawned in the George Bank area, perhaps slightly north of the western part of the bank proper. Needler's study (1930) of age and length composition and growth rates showed Passamaquoddy and Georges Bank haddock to be closely related. Needler's tag-return data, as well as recent unpublished United States and Canadian tag-return data, further show that Passamaquoddy haddock generally move south in the winter.

Browns Bank, Digby, Lockeport, LaHave and Sambro Banks, St. Margarets Bay, Canso Bank, Middle Ground, and Quereau Bank.—Average vertebral numbers fit well to the curve for haddock of these grounds indicating that they reside as adults near their original birthplace. In a study of greatly increased haddock catches in the western Nova Scotian area in 1938, McKenzie and Homans (1939) found subnormal numbers of vertebrae, indicating recruitment from New England stocks. Thus, occasional movement of New England haddock via the shoal water of the Bay of Fundy to Nova Scotian waters has been shown to be a possibility. But this is the only instance of such a population shift that has been brought to our attention.

Emerald and Sable Island Banks, Ingonish, and Southern Gulf of St. Lawrence.—Averages do not fit the curve well for haddock of these haddock grounds indicating that they have been hatched in an area where spawning temperatures

would average about 33.5° F. rather than in the areas where they were caught. Waters of this temperature may be found over certain of the eastern Nova Scotian Banks. Our method would indicate therefore that these four groups of haddock have a common birthplace on the eastern part of the Scotian Shelf where temperatures from 33° to 34° F. are to be expected during the spawning period. This conclusion is partially substantiated by the tag studies of Needler (1930), who discovered that haddock appearing on the eastern Nova Scotian Banks during the Spring spawning period migrated in summer and fall to the Ingonish area and into the Gulf of St. Lawrence.

We now have sufficient evidence to reexamine the problem of grouping northwestern Atlantic haddock into major subdivisions. The discussion of individual fishing grounds suggests that more than three independent units (New England stock, Nova Scotian stock, and Newfoundland stock) may be recognized. If we group the grounds on the basis of vertebral averages, a redefinition of the major units is suggested.

The choice of words to be used in defining population units is always difficult, and we chose not to concern ourselves too greatly with the semantics of such terminology. We shall follow the nomenclature suggested by Marr (1957), and describe our subdivisions as "stocks."

The five major units of the northwestern Atlantic haddock population which may at present be identified are as follows:

1. The Newfoundland stock, which can be clearly separated from all others on the basis of the very low number of vertebrae of haddock from St. Pierre Bank and vicinity. As samples from Grand Bank proper are not available, the status of these fish must still remain in question.
2. The eastern Nova Scotian stock, which extends east to the Laurentian Channel and west to the Scotian Gulf. An inshore group on Canso Bank and Middle Ground may be distinguished from the offshore group on Emerald, Sable Island, and Quereau Banks, and in the Gulf of St. Lawrence. The differences appear too slight, however, to justify further subdivision at present.
3. The central Nova Scotian stock, which is represented in this study by the St. Margaret's Bay and Sambro Bank groups, and resides in the vicinity of the Scotian Gulf.

4. The western Nova Scotian stock, which resides in the area bounded on the east by the Scotian Gulf and on the west by the Fundian Channel. This stock includes fish from Lockport and Digby, LaHave, and Browns Banks.

5. The New England stock, which includes fish inhabiting grounds west of the Fundian Channel and along the New England coast and is represented in this study by the Georges Bank and Passamaquoddy Bay samples.

DISCUSSION

Our data do not permit us to go beyond the point of suggesting the general arrangement of stocks. The actual degree of mixing between such units of the population as we have suggested cannot be estimated from the average numbers of vertebrae and such considerations are not within the scope of this analysis. A gradual mixing of substantial proportions of adjoining stocks of postplanktonic stages, however, should cause the vertebral numbers of the older ages to differ less than those of the younger ages. An increase in vertebral averages would be shown for the more southerly stock, and the reverse would be shown for the more northerly stock. This was not true for our year-class samples from Georges or Browns Banks, however, and the relation between temperature and vertebrae remained constant through the range of ages.

Whether refinement of our method will permit more precise identification of components of the major stocks must await the results of further research that is now in progress. Recent success in tagging haddock offshore should provide direct evidence on the question of intermixture of units.

Direct confirmation of our vertebral number-temperature relationship must await experimental hatching and rearing. Haddock eggs are known to develop in water as cold as 30° F. and as warm as 60° F. (personal communication, John B. Colton, Jr.). We could thus experimentally extend the relation past the range of our present observations which are based on natural spawning conditions.

SUMMARY

Vertebrae of haddock from 16 fishing grounds in the northwestern Atlantic were counted to de-

termine whether such counts could be used to identify population units.

Comparison of average numbers of vertebrae from the different areas showed significant differences, which could be related to surface water temperatures on the grounds during the spawning time. The relationship is consistent with that developed for northeastern Atlantic haddock from published European data.

Age data which were available for the samples from Georges and Browns Banks demonstrated that the differences in average vertebral numbers among the individual year classes on each bank could be attributed to differences in temperatures in the spawning period in different years.

Consideration of average vertebral numbers of the various population units suggests the following as major haddock stocks of the northwestern Atlantic: Newfoundland, eastern Nova Scotian, central Nova Scotian, western Nova Scotian, and New England.

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APPENDIX

The entire collection of vertebral counts used in this study is given by fishing ground and date in table A-1. A summary of the frequency distributions of the vertebral counts for the various fishing grounds and related statistical values is given in table A-2.

Analysis of variance was used to test differences among grounds and among samples of the same grounds. The original total of 9,985 vertebral counts composed of 108 samples from 16 grounds were used in the analysis. The results are as follows:

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total.....	9,984	9822.30
Between grounds.....	15	2112.30	140.8200	182.08
Within grounds.....	9,969	7110.00	0.7734
Between samples.....	107	145.02	1.3553	1.77
Within samples.....	9,862	7564.95	0.7671

The F value of 182.08 shows that differences among the grounds are highly significant (probability of occurrence by chance less than 0.01).

Individual tests, comparing differences between pairs of grounds, can be made with the analysis

of variance, but to make all possible comparisons between the 16 grounds is not practicable. Individual comparisons were made between units of different major stocks which are adjacent to each other but separated by the channels because these are of particular importance.

Highly significant differences were found between Georges and Browns Banks ($F=15.52$), between Sambro and Emerald Banks ($F=26.80$), and between St. Pierre and Quereau ($F=486.87$). These results indicate that population units representing different stocks but adjacent to each other and bordering on the channels are clearly distinct from each other.

The highly significant F value of 1.77 for the between-samples treatment indicates that the variation among samples for particular grounds is real, and the samples have been drawn from different populations.

Such real differences as do exist may be explained partially by seasonal and annual changes in year-class composition on the grounds. The only data available to test this hypothesis are those for which age data are available; namely, the 1950 collection for Georges and Browns Banks. These data are shown in text table 3. Analysis-of-variance treatments showed that the differences between individual year classes on Georges Bank were highly significant ($F=4.63$). The year classes on Browns Bank did not differ significantly ($F=1.82$), although the magnitude of difference was even greater for Browns than for Georges year classes. We would expect such differences to occur on other grounds as well.

Year-class composition on any ground will change with time. The mean vertebral number can also be expected to change since it depends on the proportion of various year classes represented. This is the most probable explanation for the significant difference between samples.

TABLE A-1.—Vertebral-number frequencies of haddock, by fishing ground and date of collection

Fishing ground and date of collection	Number of fish with vertebrae totaling—								Total
	50	51 ^a	52	53	54	55	56	57	
Georges Bank:									
November 1932		1	19	55	32	2			109
June 1935			8	36	18	1			63
Do			1	10	10	1			22
Do			9	27	14	1			51
Do			3	20	15	5			43
February 1939		4	50	172	110	10	1		347
March 1940				4	2				6
April 1950		2	23	113	105	18	1		262
August 1950		7	72	327	254	49	1		712
Total	2	14	185	764	560	87	3		1,615
Passamaquoddy Bay:									
July-August 1933			6	14	13	2			35
September 1933	1	2	19	55	39	5	2		123
Total	1	2	25	69	52	7	2		158
Digby:									
December 1933			7	14	24	5			50
October 1934		2	13	46	50	20			131
December 1935	1	1	13	65	37	6	1		124
May 1936			9	44	48	14	1		116
Total	1	3	42	169	159	45	2		421
Browns Bank:									
April 1935		1	17	72	64	18			173
July 1936			2	12	6				20
March 1939		1	16	67	54	10	1		149
March 1949			2	2	3	1			8
May 1950		3	5	69	64	22	2		165
August 1950		1	20	76	92	15			204
Total		6	62	298	283	66	4		719
La Have:									
June 1936			4	5	9	1	1		20
Lockeport:									
December 1930		3	9	34	25	19	5		95
November 1934		1	10	39	40	13	1		104
Total		4	19	73	65	32	6		199
Sambro:									
July 1933			2	10	10	3			25
October 1934			5	30	50	17	2		104
Total			7	40	60	20	2		129
Halifax and St. Margaret's Bay:									
July-August 1932			2	10	7	10	3		32
July-October 1932		1	4	48	64	45	9		171
June-September 1933			3	17	24	11	3		58
July 1933			5	23	26	18	3		75
August 1933		1	8	29	34	10	1		83
November 1934		1	5	16	18	8	3		51
Do		1	5	28	19	3	1		57
Do		1	5	11	18	12	2		49
Do			1	18	20	9	1		49
December 1934			9	27	32	17	6		91
May 1935		2	8	39	65	37	6		157
Do			4	30	60	21	5	1	121
Do			7	30	38	30	2	2	109
Do			6	19	43	29	4	1	102
Total		7	72	345	468	260	49	4	1,205
Emerald Bank:									
September 1934			1	10	7	5	1		24
January 1935			2	7	23	20	4		56
Do			2	17	64	36	4		123
February 1935			3	12	47	30	5		97
Do			5	24	65	47	7		148
Do			3	16	46	38	3		106
Do			3	18	39	23	5		88
March 1935			3	16	43	28	10		100
Do			3	12	45	31	5		96
Do			2	14	50	32	4		102
April 1935			3	28	73	60	10		174
Do			1	10	40	36	6		93
May 1935		2	1	8	36	25	2		74
Do			1	15	51	29	4		100
Do				19	40	34	6		99
June 1935			5	20	46	22	2		95
March 1936		1	4	20	39	32	2		98
Do			5	31	63	39	4		142
April 1936			5	21	38	21	4		89
Total		3	52	318	855	588	88		1,904
Sable Island:									
August 1933			1	12	44	42	2		101
September 1934			3	30	74	64	0		180
Do		1	2	32	65	39	8	2	149
Do			4	17	37	39	1	1	99

TABLE A-1.—Vertebral-number frequencies of haddock, by fishing ground and date of collection—Continued

Fishing ground and date of collection	Number of fish with vertebrae totaling—							Total	
	50	51	52	53	54	55	56		57
Sable Island—Continued									
October 1934.....		1	1	35	65	52	8		162
Do.....			2	17	44	26	4		93
Do.....			1	10	32	31	6		80
Do.....			3	19	23	23	6		79
November 1934.....			1	10	14	12	2		39
Do.....				6	20	8	1		35
Do.....			1	6	28	22			57
Do.....			6	16	22	21	3		68
Do.....				5	20	12			37
Do.....			2	8	14	11			35
July 1935.....		1	1	10	23	21	5		66
Do.....		1	2	19	63	15	7	1	108
Do.....				23	43	26	4		96
February 1936.....			2	17	74	40	4	1	138
Total.....		4	32	292	715	504	70	5	1,622
Middle Ground:									
October 1934.....			2	17	65	37	1		122
August 1935.....		4	17	52	106	69	4	1	253
April 1936.....			1	12	40	45	1		99
Total.....		4	20	81	211	151	6	1	474
Canso Bank and Petit Degrat:									
July 1934.....			2	7	10	4	3		26
November 1934.....			1	2	8	5			16
Nov.-Dec. 1934.....		1	5	27	35	23	1	1	93
June 1935.....		1	1	11	25	12	3		53
November 1935.....		1	2	14	42	31	1	1	92
June 1936.....			3	5	29	15	4	1	57
Total.....		3	14	66	149	90	12	3	337
Quereau Bank:									
November 1934.....			1	10	14	8	2		35
December 1934.....			4	18	45	26	6		99
Do.....			6	14	40	30	8	2	100
Do.....			6	29	65	37	5		142
Total.....			17	71	164	101	21	2	376
Ingonish:									
June 1935.....		2	5	24	77	37	8	1	154
Do.....			6	24	59	38	11		138
May 1936.....			4	14	39	36	6		99
Do.....		1	1	17	65	53	6	1	144
Do.....			2	20	59	50	8		139
Do.....			5	13	45	30	5		98
Total.....		3	23	112	344	244	44	2	772
Southern Gulf of St. Lawrence:									
November 1934.....				3	12	4			19
November 1935.....			3	14	39	33	3		92
Do.....				10	10	15			35
Total.....			3	27	61	52	3		146
St. Pierre Bank and vicinity:									
June 1934.....		2	4	7	1				14
November 1934.....		3	24	48	21	4			100
Do.....		1	2	28	37	3			100
Do.....			13	37	28	17	2		97
Do.....		1	2	21	57	15	1		97
Do.....			2	15	19	9			45
December 1934.....			5	28	45	26			104
June 1935.....			3	21	35	17		1	77
July 1935.....					125				125
Do.....					156				156
July 1936.....		3	21	59	12	1			96
Do.....		2	28	44	19	2	2		97
Do.....			7	32	61	18	4		122
Total.....	2	44	259	721	184	17	3		1,230

TABLE A-2.—Vertebral-number frequencies of haddock from fishing grounds of the northwestern Atlantic and related statistical values

Area	Number of fish with vertebrae totaling—								n	\bar{x}	S	$S\bar{x}$
	50	51	52	53	54	55	56	57				
NEW ENGLAND:												
Georges Bank	2	14	185	764	560	87	3		1,615	53.32	0.7965	0.0198
Passamaquoddy Bay	1	2	25	89	52	7	2		158	53.25	.9099	.0724
WESTERN NOVA SCOTIA:												
Digby	1	3	42	189	159	45	2		421	53.48	.8742	.0427
Browns Bank	0	6	62	298	283	66	4		719	53.58	.8477	.0316
LaHave Bank ¹			4	5	9	1	1		20	53.50		
Lockeport		4	19	73	65	32	6		199	53.60	1.0298	.0730
CENTRAL NOVA SCOTIA:												
Sambro Bank			7	40	60	20	2		129	53.77	.8338	.0734
St. Margaret's Bay		7	72	345	468	260	49	4	1,205	53.88	.9866	.0284
EASTERN NOVA SCOTIA:												
Emerald Bank		3	52	318	855	588	88	1	1,905	54.18	.8706	.0199
Sable Island Bank		4	32	292	715	504	70	5	1,622	54.18	.8721	.0216
Middle Ground		4	20	81	211	151	6	1	474	54.07	.8952	.0411
Canso Bank		3	14	86	149	90	12	3	337	54.06	.9651	.0525
Quereau Bank			11	42	99	64	16	2	234	54.16	.9849	.0644
Ingonish		3	29	141	409	281	49	2	914	54.19	.9033	.0269
So. Gulf of St. Lawrence			3	27	61	52	3		146	54.17	.8263	.0684
NEWFOUNDLAND:												
St. Pierre Bank and vicinity	2	44	259	721	184	17	3		1,230	52.90	.7648	.0224

¹ Statistical values not computed for this small sample.

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

BUREAU OF COMMERCIAL FISHERIES, Donald L. McKernan, *Director*

ANNOTATED BIBLIOGRAPHY ON BIOLOGY OF AMERICAN MENHADEN

By JOHN W. REINTJES, JAMES Y. CHRISTMAS, JR.,
and RICHARD A. COLLINS



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ABSTRACT

A bibliography pertaining to the biology of the menhaden, genus *Brevoortia*, including the seven species reported from North and South American waters. Included are references occurring in scientific or technical literature and duplicated reports of established series published before and during 1957. Brief annotations and a subject index are included.

ANNOTATED BIBLIOGRAPHY ON BIOLOGY OF AMERICAN MENHADEN

By JOHN W. REINTJES, *Fishery Research Biologist*, JAMES Y. CHRISTMAS, JR., *Marine Biologist*, and RICHARD A. COLLINS, *Marine Biologist*, BUREAU OF COMMERCIAL FISHERIES

When biological studies of the Atlantic menhaden resource were undertaken in 1955 by the Menhaden Investigations of the U.S. Fish and Wildlife Service, and studies of the gulf menhaden resource in 1957 by the Gulf Coast Research Laboratory under U.S. Fish and Wildlife Service contract No. 14-19-008-9335, it was recognized that a review of the literature was fundamental in planning the research program. This bibliography was therefore prepared to assist investigators in the conduct of these studies.

The bibliography deals chiefly with the American menhaden, *Brevoortia tyrannus* (Latreille), and the gulf menhaden, *B. patronus* Goode, the species of greatest importance to the menhaden industry of the United States. Three additional species occurring in North American waters are included: *B. smithi* Hildebrand, a distinct species of minor importance in the south Atlantic region; *B. gunteri* Hildebrand, a similar and distinct species of minor importance in the Gulf of Mexico; and *B. brevicaudata* Goode, a questionable species described from a single collection made at Noank, Conn., in 1874. Two additional species, *B. aurea* (Agassiz) and *B. pectinata* Jenyns, have been reported from the Atlantic coast of South America; the few references, pertaining to these species, that were available to the authors have been included.

Two genera, *Ethmidium* Thompson from the Pacific coast of South America and *Ethmalosa* Regan from the Atlantic coast of Africa, although closely allied to the menhaden, have not been included unless reported as *Brevoortia*.

In review of the literature, certain criteria were used to distinguish references that were to be included from those that were to be excluded from the work. In general, references pertaining to distribution, occurrence, abundance, life history, morphology, ecology, and behavior were included. References concerned with the technological aspects of the fishery and the reduction industry;

daily, monthly, or annual landing reports and statistics; and popular accounts in trade journals, newspapers, and magazines generally were excluded. Included are references occurring in scientific and technical literature published before and during 1957. A few references published in 1958 have been included. Generally, administrative or project progress reports have been omitted. Mimeographed or similarly duplicated reports of an established series, when principally concerned with the menhaden, have been included.

Literature respecting the menhadens contains relatively few major contributions. Many of the references make only a brief mention or listing of the species, but since the name often occurs in an index it was considered advisable to include all entries, with annotations, to guide the investigator.

The arrangement of the references is by authors, listed alphabetically. If there is more than one author, entry is made only under the senior author's name. Each author's works are listed chronologically by year of publication, and those published in the same year are given alphabetical sequence by title. Generally, pagination is given only for the parts of the publication falling within the scope of the bibliography furnishing information on the extent of the reference material. Very brief annotations of the contents of the publications are included except those whose titles give a clear indication of the contents. Because the majority of the references concern the Atlantic menhaden, or menhaden generally, annotations on species are given only when species other than *B. tyrannus* are concerned.

Acknowledgement is made of the assistance given the authors by the library staffs of the Department of the Interior, U.S. National Museum, Library of Congress, Tulane University, New Orleans Public Library, and the University of Texas, and staff members of the Marine Laboratory of the Texas Game and Fish Commission, Rockport, Tex., Gulf Fishery Investigations, Galveston, Tex., and U.S. Fishery Laboratory, Beaufort, N.C.

NOTE.—John W. Reintjes, U.S. Fish and Wildlife Service, Beaufort, N.C.; James Y. Christmas, Jr., and Richard A. Collins, Gulf Coast Research Laboratory, Ocean Springs, Miss.

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LIST OF ABBREVIATIONS OF PERIODICAL TITLES

- Amer. Fish. Soc. Spec. Publ.—American Fisheries Society. Special Publication. Ann Arbor.
- Amer. Jour. Physiol.—American Journal of Physiology. Baltimore.
- Amer. Midl. Nat.—American Midland Naturalist. Notre Dame.
- Amer. Month. Mag and Crit. Rev.—American Monthly Magazine and Critical Review. New York.
- Amer. Mus. Nat. Hist.—American Museum of Natural History. New York.
- Amer. Nat.—The American Naturalist. New York.
- Anal. Mus. Nac. Buenos Aires—Anales Museo Nacional de Historia Natural de Buenos Aires. Buenos Aires.
- Ann. Mag. Nat. Hist.—Annals and Magazine of Natural History. London.
- Ann. Rept. Dept. Mar. Fish. Canada—Annual Report of the Department of Marine Fisheries of Canada. Ottawa.
- Ann. Rept. N.J. State Mus.—Annual Report of the New Jersey State Museum. Trenton.
- Ann. Rept. N.Y. Comm. Fish.—Annual Report, New York Commissioner of Fisheries. Albany.
- Ann. Rept. N.Y. Cons. Dept.—Annual Report of the New York Conservation Department. Albany.
- Ann. Rept. N.Y. Forest, Fish and Game Comm.—Annual Report of the New York Forest, Fish and Game Commission. Albany.
- Ann. Rept. N.Y. State Mus.—Annual Report New York State Museum. Albany.
- Ann. Rept. R.I. Comm. Inl. Fish.—Annual Report of the Rhode Island Commissioner of Inland Fisheries. Providence.
- Ann. Rept. Smithsn. Inst.—Annual Report of the Smithsonian Institution. Washington.
- Arq. Zool. Sao Paulo—Arquivos de Zoologia do Estado de São Paulo. São Paulo.
- Biol. Bull.—Biological Bulletin. Marine Biological Laboratory. Woods Hole.
- Bost. Jour. Nat. Hist.—Boston Journal of Natural History. Boston.
- Bull. Amer. Mus. Nat. Hist.—Bulletin of the American Museum of Natural History. New York.
- Bull. Bingham Oceanogr. Coll.—Bulletin of the Bingham Oceanographic Collection. Yale University. New Haven.
- Bull. Fla. State Mus.—Bulletin of the Florida State Museum. Gainesville.
- Bull. La. Dept. Cons.—Bulletin of the Louisiana Department of Conservation. New Orleans.
- Bull. Mus. Comp. Zool.—Bulletin of the Museum of Comparative Zoology. Harvard College. Cambridge.
- Bull. N.Y. State Mus.—Bulletin of the New York State Museum. Albany.
- Bull. Soc. Cent. Aquic. Peche.—Bulletin de la Société centrale d'aquiculture et de Pêche. Paris.
- Bull. Tex. Game, Fish and Oyster Comm.—Bulletin of the Texas Game, Fish and Oyster Commission. Rockport.
- Bull. U.S. Bur. Fish.—Bulletin of the United States Bureau of Fisheries. Washington.
- Bull. U.S. Fish Comm.—Bulletin of the United States Fish Commission. Washington.
- Bull. U.S. Natl. Mus.—Bulletin of the United States National Museum. Washington.
- Canad. Nat.—Canadian Nature. Toronto.
- Canad. Nat. and Geol.—Canadian Naturalist and Geologist. Ottawa.
- Chesapeake Biol. Lab. Publ.—Chesapeake Biological Laboratory. Publication. Maryland Department of Research and Education. Solomons.
- Comm. Fish. Rev.—Commercial Fisheries Review. United States Fish and Wildlife Service. Washington.
- Cons. Bull. U.S. Fish Wildlife—Conservation Bulletin, United States Fish and Wildlife Service. Washington.
- Cons. Internat. Explor. de la Mer, Rapp. et Proc. Verb.—Conseil Permanent International pour L'exploration de la Mer, Rapports et Procès-Verbaux des Réunions. Copenhagen.
- Contr. Canad. Biol.—Contributions to Canadian Biology. Canadian Biological Board. Toronto.
- Ecol. Monogr.—Ecological Monographs. Ecological Society of America. Duke University Press. Durham.
- Ecology—Ecological Society of America. Duke University Press. Durham.
- Exp. Parasit.—Experimental Parasitology. Academic Press Inc. New York.
- Fla. Bd. Cons. Educ.—Florida Board of Conservation and Education. Tallahassee.
- Fla. State Mus.—Florida State Museum. Tallahassee.
- Fish. Bull. U.S. Fish Wildlife—Fishery Bulletin, United States Fish and Wildlife Service. Washington.
- Geogr. Rév.—Geographic Review. New York.
- Great Int. Fish. Exhb.—Great International Fisheries Exhibit. London.
- Hull Bull. Mar. Ecol.—Hull Bulletin of Marine Ecology, Hull University College, Hull.
- Ill. Biol. Monogr.—Illinois Biological Monographs. Urbana.
- Inv. Rept. U.S. Bur. Fish.—Investigational Report, United States Bureau of Fisheries. Washington.
- Jour. Acad. Nat. Sci. Phila.—Journal of the Academy of Natural Sciences. Philadelphia.
- Jour. Biol. Chem.—Journal of Biological Chemistry. Baltimore.
- Jour. Elisha Mitchell Sci. Soc.—Journal of the Elisha Mitchell Scientific Society. Chapel Hill.

- Jour. Mar. Biol. Assn. (U.K.)—Journal of the Marine Biological Association of the United Kingdom. Plymouth.
- Jour. Parasitol.—Journal of Parasitology. Lancaster.
- Jour. Wash. Acad. Sci.—Journal of the Washington Academy of Sciences. Washington.
- Jour. Wildlife Mgt.—Journal of Wildlife Management. Washington.
- La. Cons. Rev.—Louisiana Conservation Review. New Orleans.
- Limnol. Oceanogr.—Limnology and Oceanography. American Society of Limnology and Oceanography. Baltimore.
- Mar. Life Occ. Pap.—Marine Life Occasional Papers. New York.
- Md. Cons. Bull.—Maryland Conservation Bulletin. Annapolis.
- Mem. Amer. Acad. Arts Sci.—Memoirs of the American Academy of Arts and Science. Boston.
- Miss. Seafood Comm.—Mississippi Seafood Commission. Biloxi.
- Monogr. Acad. Nat. Sci. Phila.—Monographs of the Academy of Natural Sciences. Philadelphia.
- Nat. Hist. Soc. Md. Bull.—Natural History Society of Maryland Bulletin. Baltimore.
- Natl. Fish. Inst.—National Fisheries Institute. Washington.
- N.C. Geol. Econ. Sur.—North Carolina Geological and Economic Survey. Raleigh.
- N.Y. Cons. Dept.—New York Conservation Department. Albany.
- N.Y. Fish and Game Jour.—New York Fish and Game Journal. Albany.
- N.Y. State Dept. Cons.—New York State Department of Conservation. Freeport.
- Occ. Pap. Boston Soc. Nat. Hist.—Occasional Papers of the Boston Society of Natural History. Boston.
- Occ. Pap. Mar. Lab. La. State Univ.—Occasional Papers of the Marine Laboratory, Louisiana State University. Baton Rouge.
- Occ. Pap. Mus. Zool. Mich.—Occasional Papers of the Museum of Zoology, University of Michigan. Ann Arbor.
- Oceanogr. Inst. Fla. State Univ.—Oceanographic Institute of the Florida State University. Tallahassee.
- Öfvers. Svensk. Vet. Akad. Förh.—Öfversigt af Svenska Vetenskapsakademien Förhandlingar. Stockholm.
- Proc. Acad. Nat. Sci. Phila.—Proceedings of the Academy of Natural Sciences. Philadelphia.
- Proc. Amer. Phil. Soc.—Proceedings of the American Philosophical Society. Philadelphia.
- Proc. Biol. Soc. Wash.—Proceedings of the Biological Society of Washington. Washington.
- Proc. Boston Soc. Nat. Hist.—Proceedings of the Boston Society of Natural History. Boston.
- Proc. Central Fish Cult. Soc.—Proceedings of the Central Fish Cultural Society. Washington.
- Proc. Gulf Carib. Fish. Inst.—Proceedings of the Gulf and Caribbean Fisheries Institute. Coral Gables.
- Proc. Portland Soc. Nat. Hist.—Proceedings of the Portland Society of Natural History. Portland.
- Proc. Trans. Nova Scotian Inst. Nat. Sci.—Proceedings and Transactions of the Nova Scotian Institute of Natural Sciences. Halifax.
- Proc. U.S. Natl. Mus.—Proceedings of the United States National Museum. Washington.
- Proc. Zool. Soc. London.—Proceedings of the Zoological Society of London. London.
- Publ. Inst. Mar. Sci.—Publication of the Institute of Marine Science. Port Aransas.
- Quart. Jour. Fla. Acad. Sci.—Quarterly Journal of the Florida Academy of Sciences. Gainesville.
- Rept. Maine Bd. Agr.—Report of the Maine Board of Agriculture. Augusta.
- Rept. Mass. Comm. Fish.—Report of the Massachusetts Commissioner of Fisheries. Boston.
- Rept. Md. Comm. Fish.—Report of the Maryland Commissioner of Fisheries. Annapolis.
- Rept. U.S. Comm. Fish.—Report of the United States Commissioner of Fisheries. Washington.
- Rept. U.S. Comm. Fish and Fisheries—Report of the United States Commissioner of Fish and Fisheries. Washington.
- Rept. State Geol. N.J.—Report of the State Geologist of New Jersey. Trenton.
- Sears Found. Mar. Res.—Sears Foundation of Marine Research, Yale University. New Haven.
- Secy. Rept. Assn. Me. Oil and Guano Mfg.—Secretary's Report of the Association of Maine Oil and Guano Manufacturers. Portland.
- Serv. Info. Agric. Brazil—Servico de informacao agricola Brazil. Rio de Janeiro.
- Smithsn. Misc. Coll.—Smithsonian Institution Miscellaneous Collection. Washington.
- Spec. Sci. Rept.: Fish. U.S. Fish Wildlife—Special Scientific Reports: Fisheries. United States Fish and Wildlife Service. Washington.
- Stanford Ichth. Bull.—Stanford Ichthyological Bulletin, Leland Stanford Jr. University. Palo Alto.
- Stud. Biol. Lab. Johns Hopkins U.—Studies of the Biological Laboratory, Johns Hopkins University. Baltimore.
- Tasca—Texas Academy of Science. Collegiate Academy. Sam Houston State College. Huntsville.
- Tex. A. and M. Res. Found.—Agricultural and Mechanical College of Texas Research Foundation. College Station.
- Tex. Game and Fish.—Texas Game and Fish. Austin.
- Tex. Game, Fish and Oyster Comm.—Texas Game, Fish and Oyster Commission. Rockport.
- Tex. Jour. Sci.—Texas Journal of Science. Austin.
- Trans. Amer. Fish. Soc.—Transactions of the American Fisheries Society. Ann Arbor.
- Trans. Amer. Microsc. Soc.—Transactions of the American Microscopical Society. Columbus.
- Trans. Amer. Phil. Soc.—Transactions of the American Philosophical Society. Philadelphia.
- Trans. Lit. Phil. Soc. N.Y.—Transactions of the Literary and Philosophical Society. New York.

Trans. No. Amer. Wildlife Conf.—Transactions of the North American Wildlife Conference. Washington.
Univ. Fla. Press—University of Florida Press. Gainesville.
Univ. N.C. Press—University of North Carolina Press. Chapel Hill.
U.S. Bur. Fish. Inv. Rept.—United States Bureau of Fisheries, Investigational Report. Washington.

U.S. Dept. Agric. Bull.—United States Department of Agriculture. Bulletin. Washington.
Va. Acad. Sci.—Virginia Academy of Sciences. Richmond.
Va. Fish. Lab.—Virginia Fisheries Laboratory. Gloucester Point.
Va. Jour. Sci.—Virginia Journal of Science. Lexington.

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 Gunter, 1938a, 1945, 1957.
 Günther, 1880.
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 Lawson, 1709.
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 Fish, 1926.
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 Gill, 1873a, 1873b.
 Ginsburg, 1952.
 Gordon, 1949, 1951.
 Gould, 1885.
 Grant, 1883.
 Greeley, 1939.
 Gudger, 1910.
 Gunter, 1945, 1956b.
 Hathaway, 1910.
 Henshall, 1895.
 Higgins and Pearson, 1927.
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 Jordan and Evermann, 1896b.
 June, 1958.
 Kendall, 1914.
 Latham, 1917a, 1917b, 1919.
 Loring, 1873.
 Lund, 1935.
 Mansueti and Scheltema, 1953.
 Massmann, 1953, 1954.
 Mazyck, 1885.
 Merriman, 1947.
 Metzelaar, 1919.
 Nichols and Breder, 1926.
 Pearson, 1941.
 Perlmutter, 1939.
 Powell, 1950.
 Raney and Massmann, 1953.
 Reid, 1957.
 Rounsefell, 1954.
 Scattergood, 1948.
 Scattergood, Trefethen, and Coffin, 1951a, 1951b.
 Sherwood and Edwards, 1902.
 Smiley, 1885b, 1887a, 1887b.
 Smith, 1892, 1893b.
 Soper, 1887.
 Southwick, 1885.
 Springer and Bullis, 1956.
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 Hargis, 1955a, 1955b, 1957.
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 Linton, 1901a, 1901b, 1904, 1908, 1925, 1940.
 Meglitsch, 1947.
 Menzel, 1956.
 Moore, 1894.
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 Rathbun, 1884, 1888.
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UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

DETERMINING AGE OF ATLANTIC MENHADEN FROM THEIR SCALES

BY FRED C. JUNE AND CHARLES M. ROITHMAYR



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ABSTRACT

Scales of Atlantic menhaden, *Brevoortia tyrannus*, are described and results of detailed examination summarized for the purpose of determining whether certain recognizable rings are reliable age marks. Based on the occurrence of one or more dominant modes in monthly frequency distributions of scale measurements of two separate ring classes, it was shown that (1) the modes representing each ring remained homologous, (2) an increase in the number of rings was accompanied by an increase in the length of the scales, (3) the distance between modes representing the last submarginal ring and the edge of the scale decreased with the addition of each new ring, (4) new scale growth was greatest during the warm months of the year, reaching a maximum in the fall, and (5) scale rings are formed only once each year and thus are reliable age marks. Differences were observed in the growth of scales from fish assigned to two different ring classes, and new scale growth was found to be greatest in southern coastal waters and in younger fish. Examination of scales from fish confined over a 14-month period showed that only one ring had formed, thus verifying the validity of the scale method.

DETERMINING AGE OF ATLANTIC MENHADEN FROM THEIR SCALES

By FRED C. JUNE and CHARLES M. ROITHMAYR, *Fishery Research Biologists*

BUREAU OF COMMERCIAL FISHERIES

Knowledge of the age of Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), is useful in solving basic life-history problems of the species and is essential to an understanding of the population dynamics of the fishery. It would be difficult, indeed, to determine the number and size of year classes in the fishable stock and to compute such vital statistics as growth rate or fishing and mortality rates without a knowledge of age. In the study of these matters, being conducted by the U.S. Fish and Wildlife Service, it is of paramount importance, therefore, that some reliable method of assessing the age of individual fish be established.

Rush (1952) examined the scales of 34 Atlantic menhaden collected at Beaufort, N. C., and calculated the lengths of the fish at the time of annulus formation from scale measurements. He concluded that the observed annulus groups, when plotted against fork length, produced a normal growth curve. Westman and Nigrelli (1955) identified the ages of specimens collected in northern New Jersey and southern Long Island waters from scales, but did not establish the validity of the readings. McHugh, Oglesby, and Pacheco (1959) demonstrated that annuli in young menhaden are formed in spring and found close correspondence in ages determined from length-frequency distributions and from scales. These efforts represent the only previous records of attempts to assess the age of this species from scales. It is the primary purpose of this paper to examine these structures in some detail to determine whether certain recognizable rings are reliable age marks.

The material on which this report was based was collected by many temporary field assistants employed by the Menhaden Investigations. Drs. J. Lawrence McHugh and George A. Rounsefell critically read the manuscript.

COLLECTION AND TREATMENT OF SCALE SAMPLES

The bulk of the scales for study was obtained from samples of purse-seine landings at various ports along the middle Atlantic coast of the United States from 1952 through 1956. Data for 1952 and 1953 came from weekly or semi-weekly samples of the catches landed at Lewes, Del., and Wildwood, N. J. In 1954, additional samples were obtained daily at Amagansett, N. Y., commencing in August, and periodically throughout the season at Port Monmouth, N. J. In 1955, samples for the most part were collected each day that purse-seine landings were made at Portland, Maine; Gloucester, Mass.; Amagansett, N. Y.; Port Monmouth, N. J.; Lewes, Del.; Reedville, Va.; Beaufort and Southport, N. C.; Yorges Island, S. C.; and Fernandina Beach, Fla. However, only a part of this great mass of data was used in the study. Scale collections also were obtained outside the regular purse-seine fishing season from pound-, fyke-, and gill-net fisheries operating along the middle Atlantic coast and in Chesapeake Bay. Additional material included periodic collections of scales from young-of-the-year fish inhabiting estuarine nursery grounds in Indian River, Delaware. Scales also were taken from fish reared over a period of 14 months in outdoor ponds at Beaufort, N. C. Results of readings of 13,510 scale samples are reported in this study.

The procedure used in sampling the purse-seine, pound-, fyke-, and gill-net fisheries involved taking random samples, each of 100 fish, from a single day's catch. The fork lengths of the fish in each sample were measured on a board having a nose block at one end and a millimeter scale inlaid along the center. Scale samples were taken from every fifth fish. Those fish from which scales were taken were weighed and the sex and stage of sexual maturity noted. Approximately 25 scales were removed from the

NOTE.—Approved for publication, May 21, 1959. Fishery Bulletin 171.

middle of the left side below the insertion of the dorsal fin (see p. 325). If scales were missing from this region, they were taken from the same location on the right side of the body; or if scales were missing from both sides, another fish of the same half-centimeter size class was substituted. Individual scale samples were placed temporarily in a 2-dram vial containing water and three or four drops of 2-percent phenol.

Scales were cleaned of integument and chromatophores by rubbing between the fingers and were mounted dry between two glass slides held together at the ends with cellulose tape. Usually six scales were mounted from each fish. Each

scale sample was identified by a serial number, the only information placed on the slide. A few of the scale samples were placed in scale books at the time of collection and subsequently soaked and cleaned prior to mounting.

An Eberbach projector was used for viewing the scales at a magnification of $40\times$. All scales were read by the authors, each reading the samples independently. One scale from each sample was selected for measurement. The scale chosen was free from defects and represented the most symmetrical scale in the sample. The distances from the proximate center of the base of the sculptured field (overlay fig. 1) to each

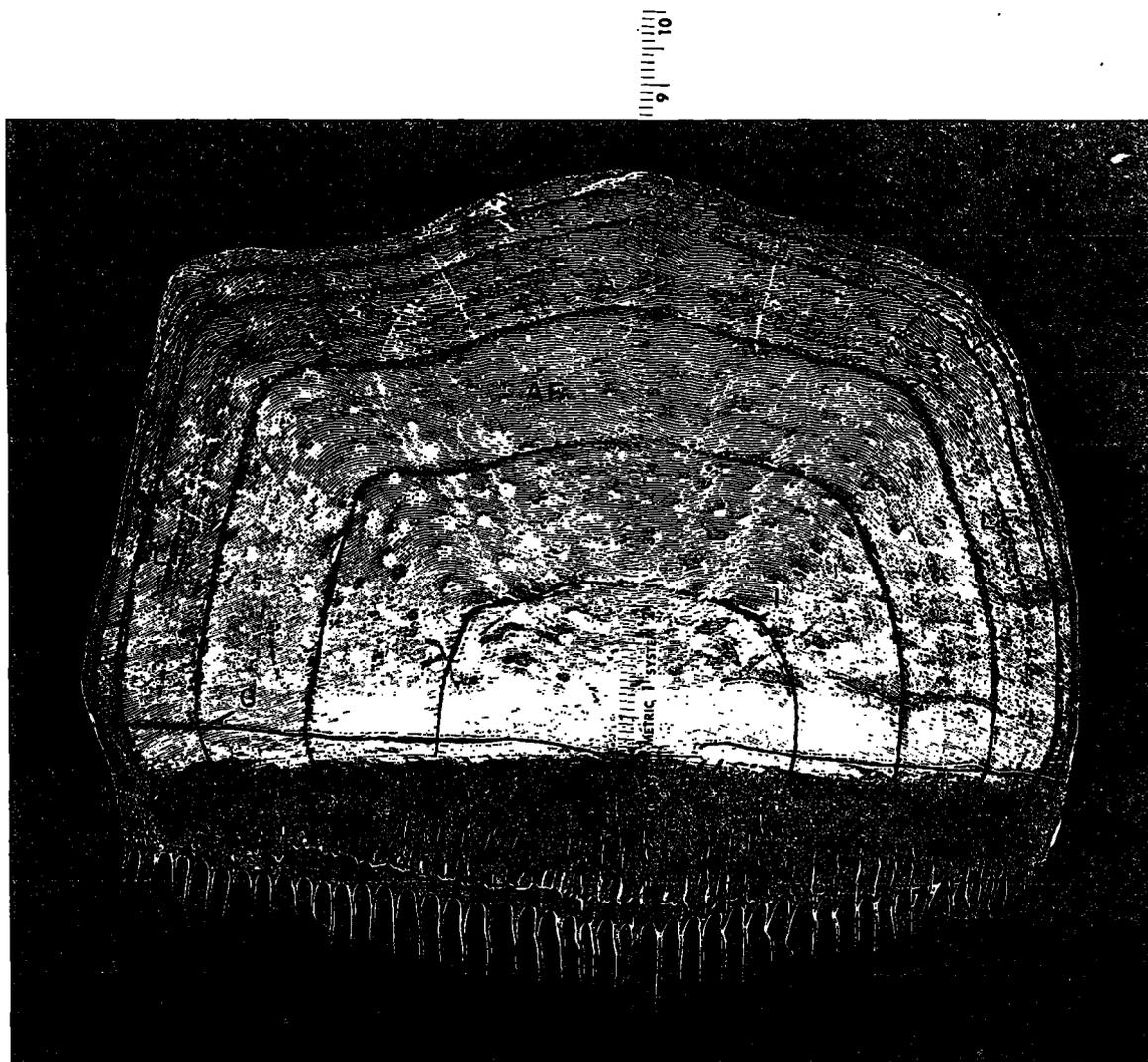


FIGURE 1.—Scale of Atlantic menhaden with five rings. AF, anterior field; PF, posterior field; LF, lateral field; SM, scale margin; G, groove; P, pectinations; R, ridges. Arabic numerals indicate age rings.

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

FISHERY BULLETIN 171

(Fishery Bulletin of the Fish and Wildlife Service, vol. 60, p. 324)

CORRECTION

In figure 1, on page 324, the tracing that identifies the parts of the scale was printed directly upon the picture instead of on a separate tissue overlay. Please insert this correctly printed picture with its tissue overlay on page 324.

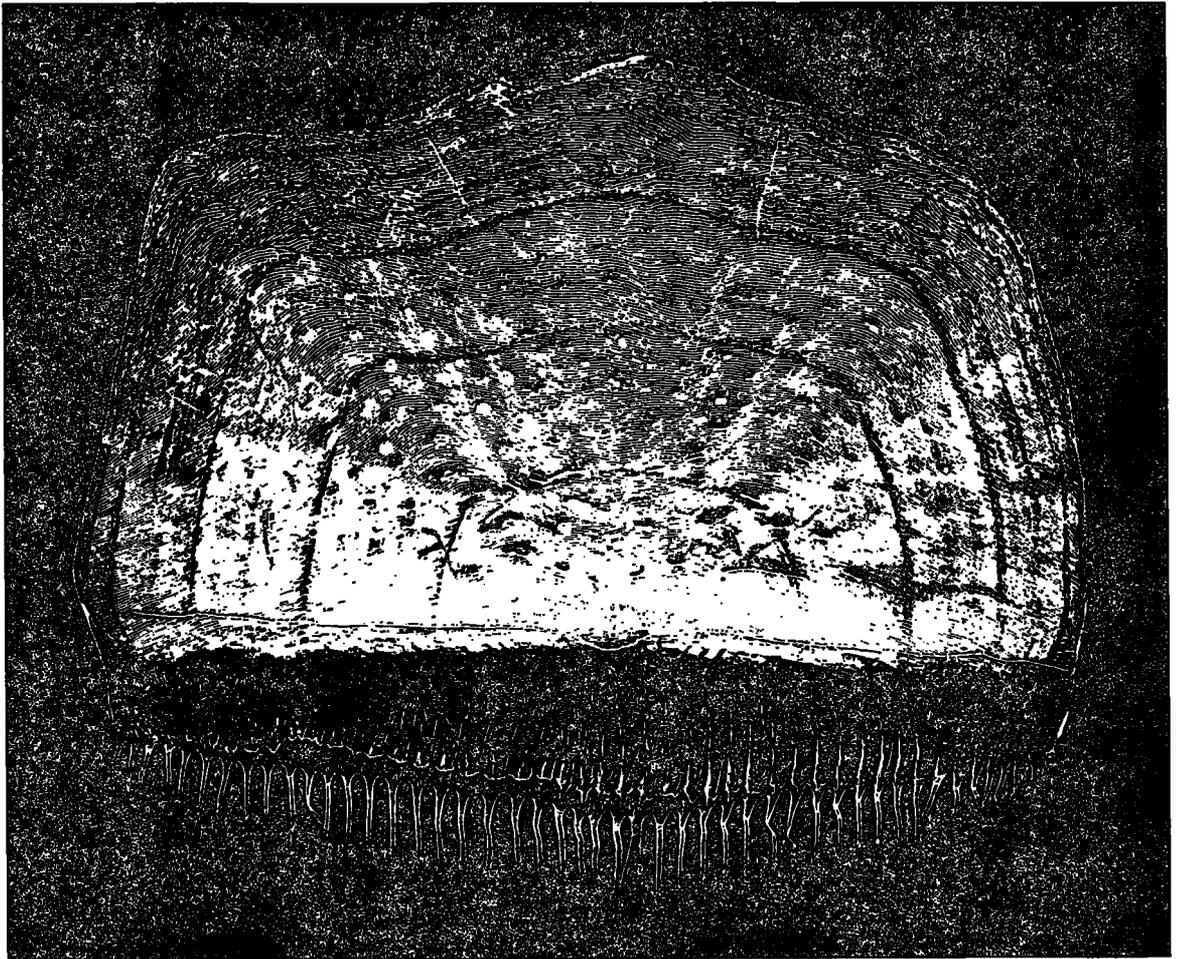


FIGURE 1.—Scale of Atlantic menhaden with five rings. See overlay for identification of parts.

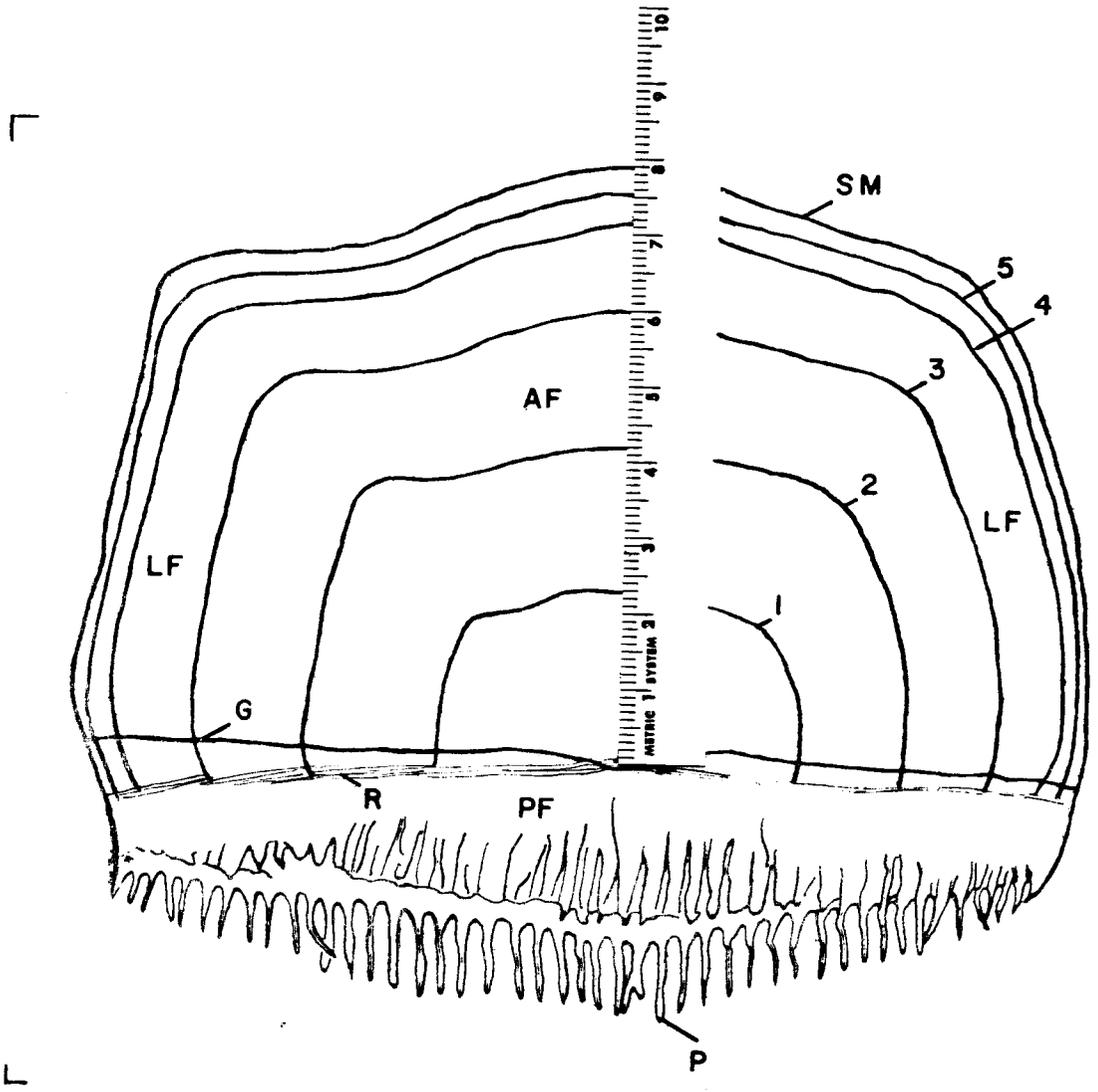


FIGURE 1—Overlay. AF, anterior field; PF, posterior field; LF, lateral field; SM, scale margin; G, groove; P, pectinations; R, ridges. Arabic numerals indicate age rings.

ring and to the margin of the scale were measured to the nearest millimeter. Measurements were marked on a Keysort card having a ruled metric scale along one edge. The independent age readings and measurements were compared and differences either reconciled or the scale samples of questionable age discarded.

DESCRIPTION OF SCALES

Scale structure in the genus *Brevoortia* indicates a specialization in development, divergent from that of most other members of the herring family. The posterior margin of the scale in young fish is serrate, in adults pectinate, and nearly vertical, whereas in most herrings the posterior margins are smooth and rounded.

In general, scales of Atlantic menhaden are adherent, translucent, and rather thin. The exposed, posterior field is granular and much deeper than long. Basal portions of the serrations or pectinations are clearly evident in this field and constitute an argument for the continual growth of the scale. The imbedded, anterior field is sculptured with ridges which run more or less parallel to the anterior margin of the scale. Usually one or more grooves cross the anterior field near and parallel to its base. In older fish, radial fissures frequently transect the anterior margin of the scale. A small, clear, somewhat semicircular area occurs at the proximate center of the base of the anterior field (fig. 1).

To determine whether differences existed among scales from various regions of the body, scale patterns of 15 fish of varying size were examined in detail. Results showed that the largest and most symmetrical scales occurred in a median, lateral band between the tip of the flexed pectoral fin and the insertion of the dorsal fin. Furthermore, rings on the scales from this region were most clearly marked. Accordingly, all scale samples were taken from this area of the body.

EARLY SCALE GROWTH

Atlantic menhaden scales begin as cycloid scales (fig. 2). Examination of stained larval and postlarval specimens collected in the vicinity of Beaufort, N. C., and in Indian River, Delaware, during the winter and spring months of

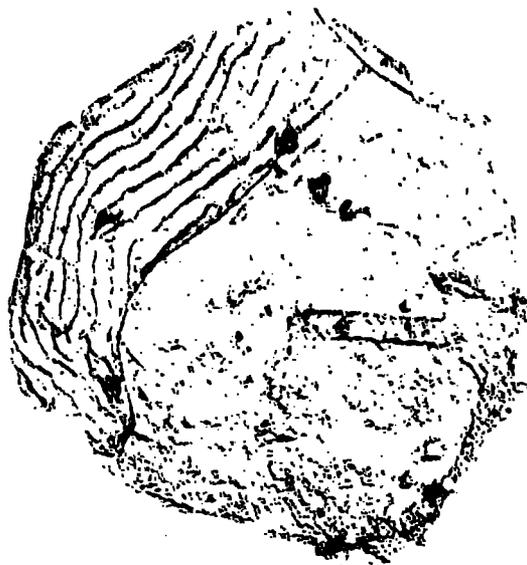


FIGURE 2.—Photomicrograph of a scale from a post-larval Atlantic menhaden.

1955 and 1956 indicated that scale formation commenced at body lengths between 24 and 30 millimeters. Detailed study of the developmental stages of larvae captured in January 1955, and reared through metamorphosis in ponds at the U.S. Fishery Laboratory at Beaufort, substantiated these findings.

Scales were first observed in the region of the caudal peduncle and along a median, lateral line on the body. Later they appeared near the base of the pectoral fins and along the posterior margin of the opercle. Appearance of the scales marks the first apparent feature of metamorphosis from larva to juvenile. In all specimens examined, the scales were fully formed at body lengths between 30 and 43 millimeters.

Growth of the scales prior to ring formation was determined from young-of-the-year fish obtained during the late spring and summer of 1956 in Indian River, Delaware. Measurements of their scale lengths are shown as percentage frequency distributions in figure 3. The first individuals from which scales could be secured were taken on May 22. The mode of the scale lengths of this group was 13 millimeters (at a magnification of 40 ×). Growth of the scales was traced until mid-September, when the mode

had progressed to 78 millimeters. All of these scales were devoid of any markings that might be interpreted as age rings (fig. 4), hence, the latter must be formed sometime after the first summer of life. Examination of many thousands of juveniles collected in other estuarine nursery areas along the Atlantic coast during the summer months of 1955 and 1956 supports this conclusion.

DEFINITION OF AN AGE RING

Recognition of age rings on Atlantic menhaden scales was based on recurrent interruptions of the uniformly spaced ridges in the anterior field. Such areas of discontinuous and irregular ridges form narrow, continuous, light bands which normally stand out in sharp contrast to the bold, continuous, and regular ridges on either side. Occasionally, such a band may

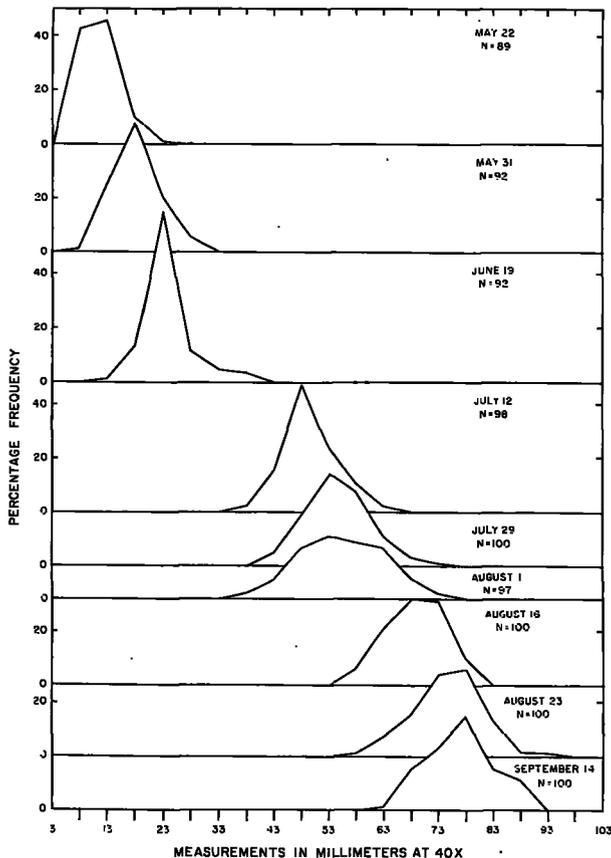


FIGURE 3.—Frequency distributions of scale-length measurements of juvenile Atlantic menhaden collected in Indian River, Delaware, in 1956.



FIGURE 4.—Scale of Atlantic menhaden with no rings.

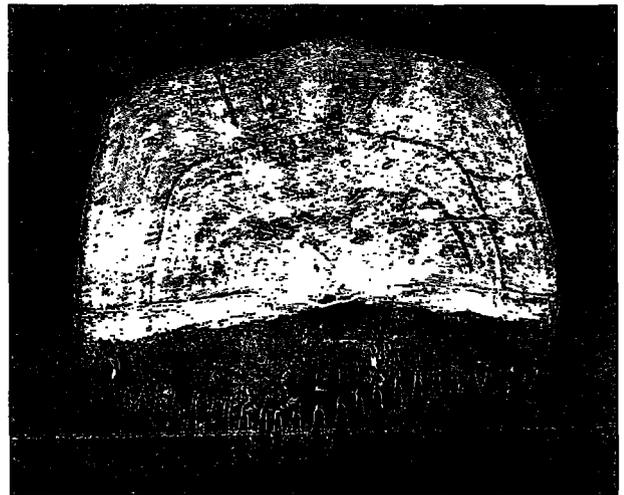


FIGURE 5.—Scale of Atlantic menhaden with one ring.

appear as a sharp line separating ridges of different elevations. These bands are separated from each other and are present in the same relative position on the scales of an individual fish. They are roughly parallel to the margin and may be traced around the entire sculptured portion of the scale. Such a band is here defined as an age ring.

Other scale features provide additional criteria for recognition of an age ring. Under magnification, the first ring usually stands out in bold relief on the posterior field, and by careful focusing, traces of additional rings may be apparent; continuations of the rings may sometimes be seen in the posterior field. Erosion of the scale at or near a ring further enhances the character of a ring (figs. 5-9).

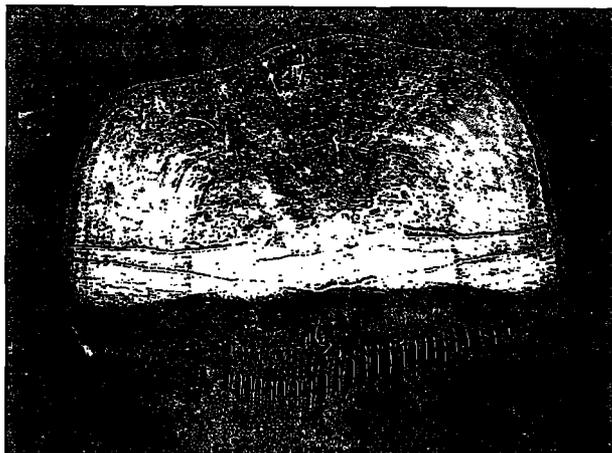


FIGURE 6.—Scale of Atlantic menhaden with two rings. The second ring is located just inside the margin.



FIGURE 7.—Scale of Atlantic menhaden with three rings.

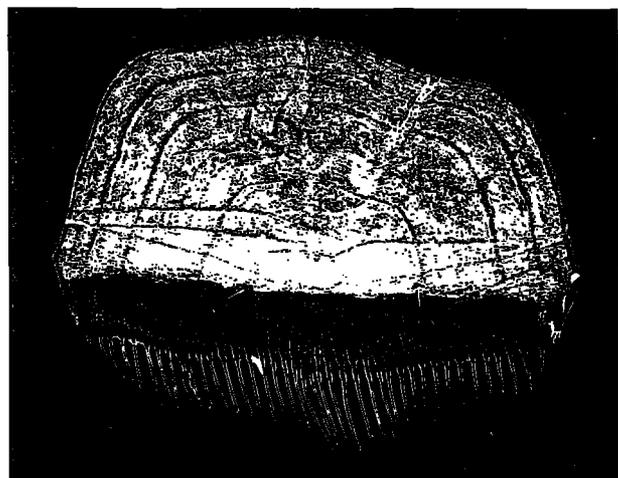


FIGURE 8.—Scale of Atlantic menhaden with four rings.

IRREGULARITIES IN SCALE STRUCTURE

Several major irregularities in scale structure occasionally occur, and these may have affected the accuracy of some of the age determinations. Most important of these is the occurrence of accessory rings, which oftentimes resemble the defined age ring, but differ in their scarlike appearance. Such rings usually are incomplete, irregular in outline, and not parallel to the margin. Accessory rings frequently appear as folds in the sculptured pattern, and the ridges crossing such folds show a continuity and regularity, rather than the discontinuity and irregularities of the defined age ring. Furthermore, they usually occur at irregular intervals between regularly spaced and clearly marked age rings (fig. 10). Finally, and most important, accessory rings rarely are present on all scales of an individual fish.

Perhaps the most common irregularity in Atlantic menhaden scales occurs in the central area of the anterior field where the distinct, regularly spaced ridges are replaced with short, discontinuous scars. Such areas generally are granular in appearance, irregular in outline, and highly variable in relative size (fig. 11). Scales with such areas were considered to be regenerated and were not used in the age determinations.

Occasionally, there appears to be a smaller scale set off center in a larger scale. The axes of the two scales are at different angles. This condition is presumed to be the result of a younger scale being dislocated and rotated slightly in the scale pocket, since subsequent scale growth is normal and along the proper axis (fig. 12).

Additional minor irregularities in structure frequently occur in scales of older fish. These include excessive erosion of the scale at or near the location of an age ring (fig. 13); scars which are granular in appearance and devoid of ridges; small, clear areas in the sculptured portion; coarse, radial fissures in the anterior field (fig. 14); and rough, granular ridges in the central region of the anterior field. These minor defects, for the most part, do not cause any difficulty in determining the location of an age ring and normally do not occur on all scales of an individual.

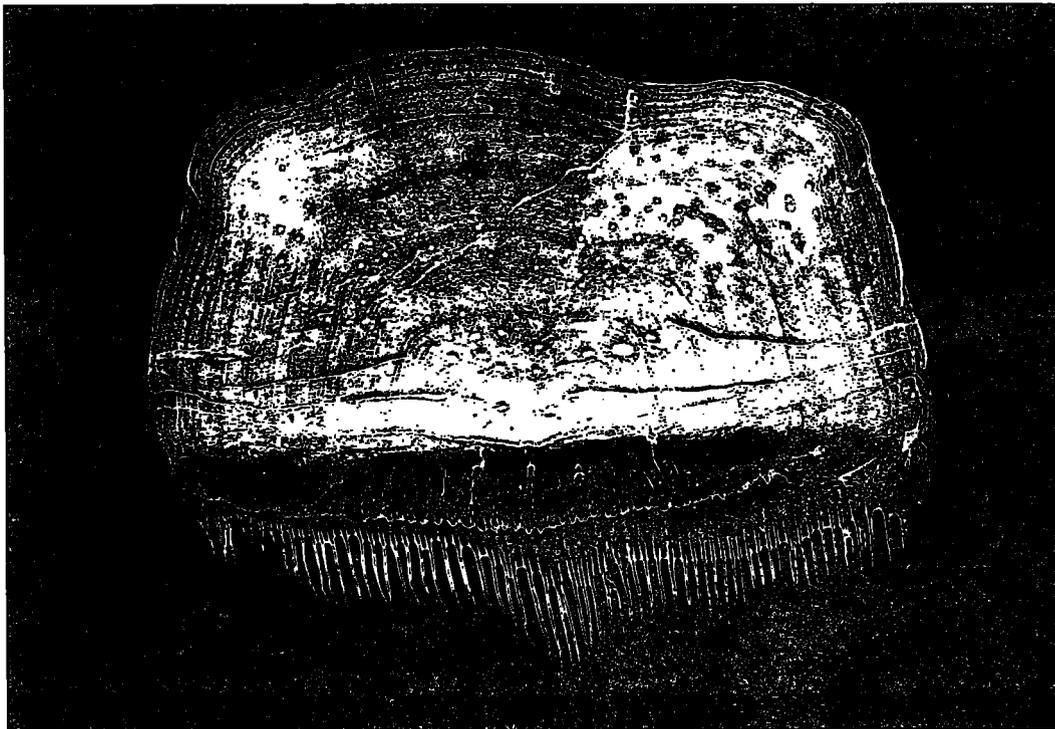


FIGURE 9.—Scale of Atlantic menhaden with 10 rings.

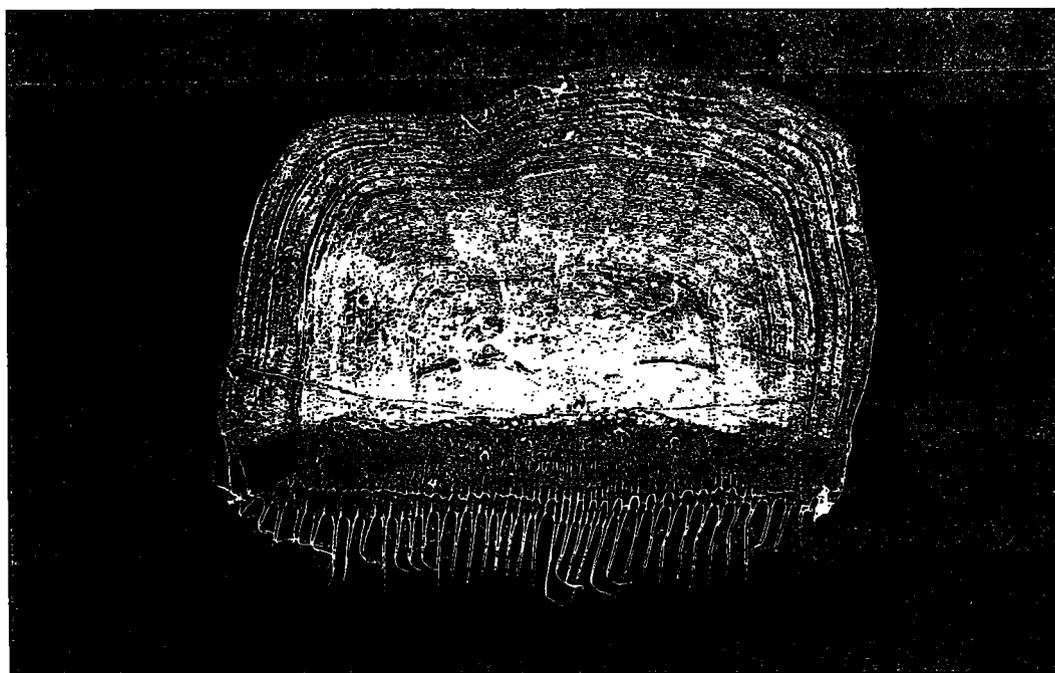


FIGURE 10.—Scale of Atlantic menhaden with three age rings and several accessory, or false, rings.

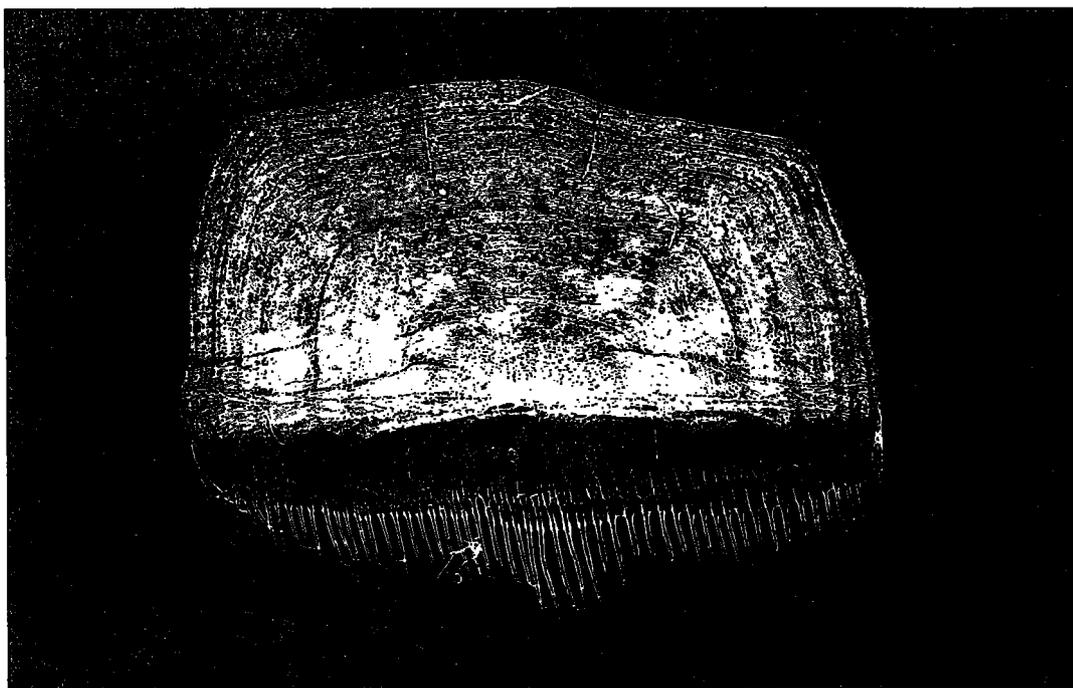


FIGURE 11.—Scale showing a regenerated central area.

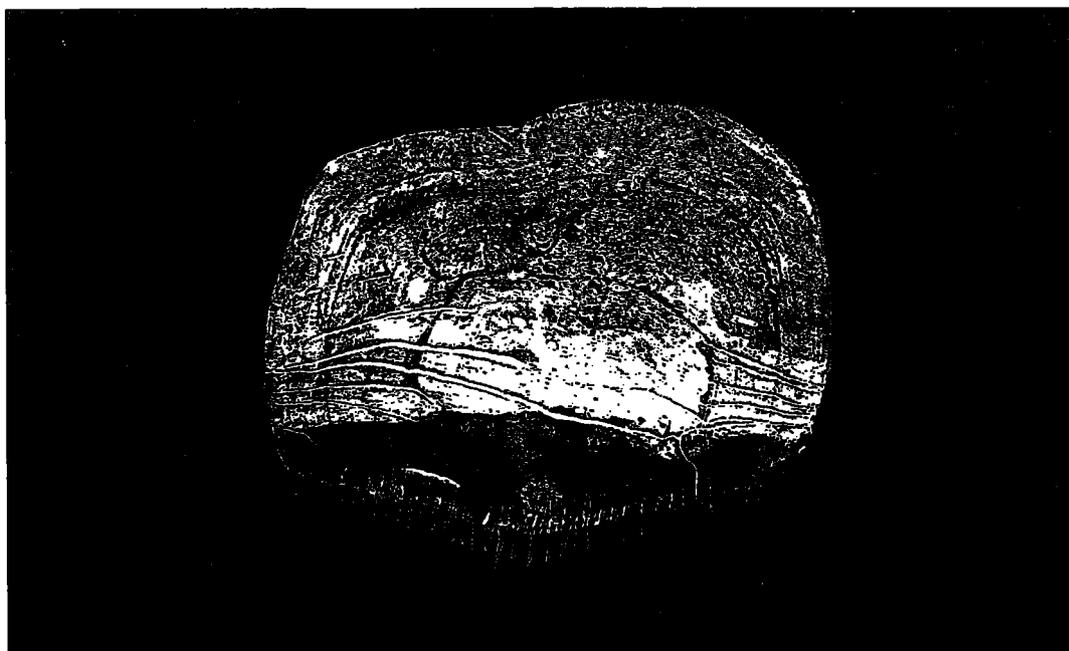


FIGURE 12.—Scale showing a rotated central area.

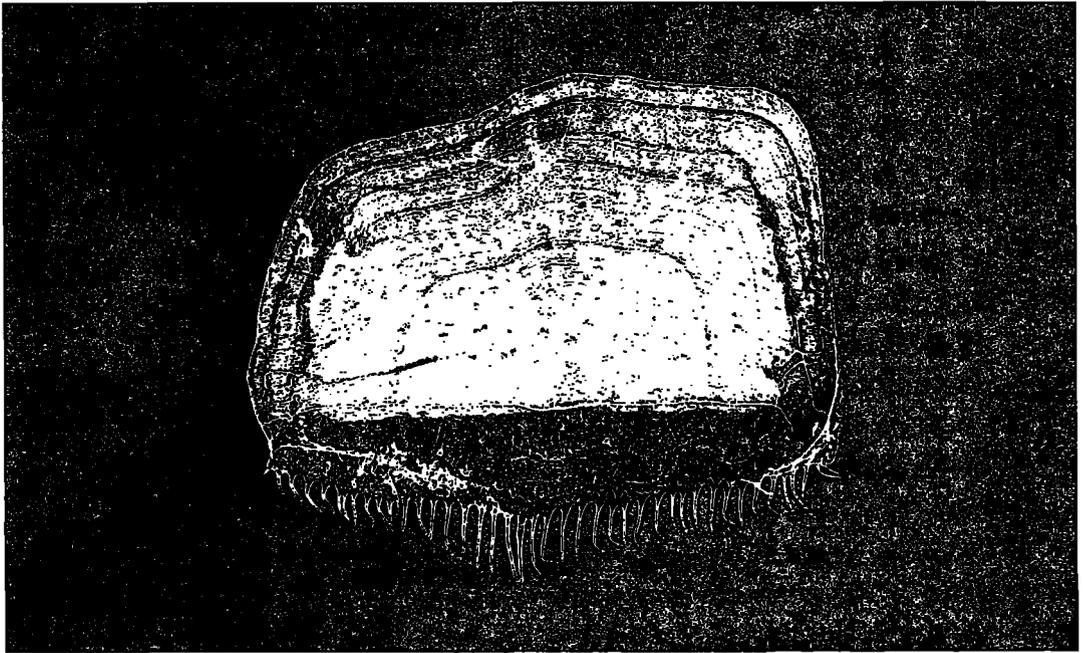


FIGURE 13.—Scale showing erosion at the location of an age ring.

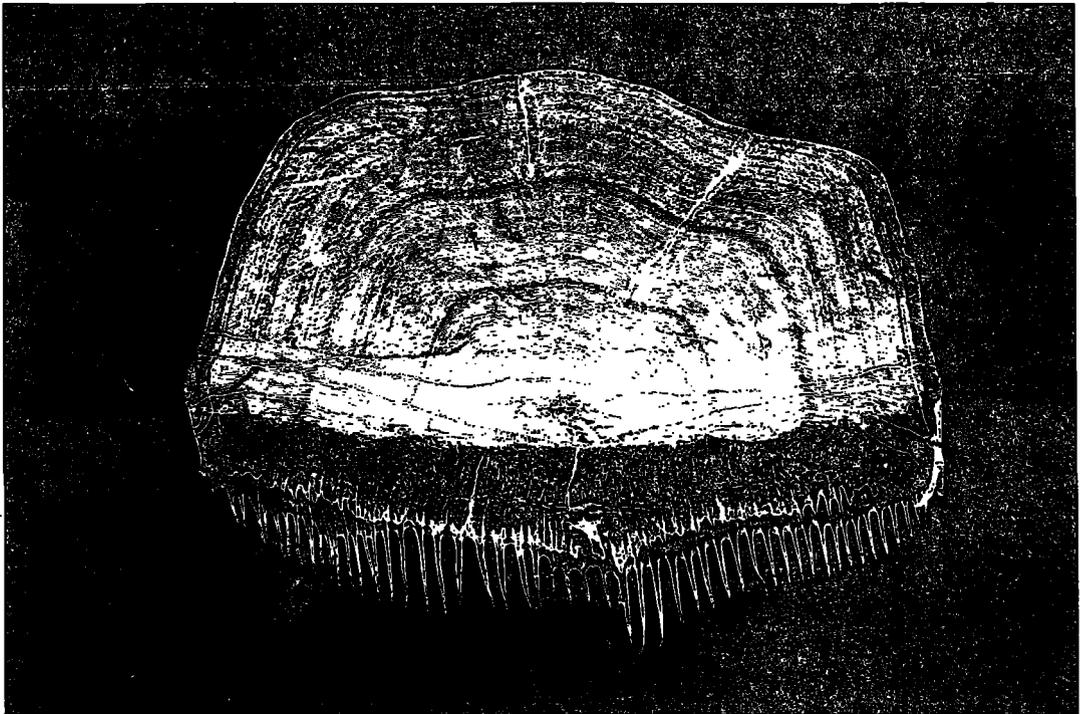


FIGURE 14.—Scale showing radial fissures in the anterior field.

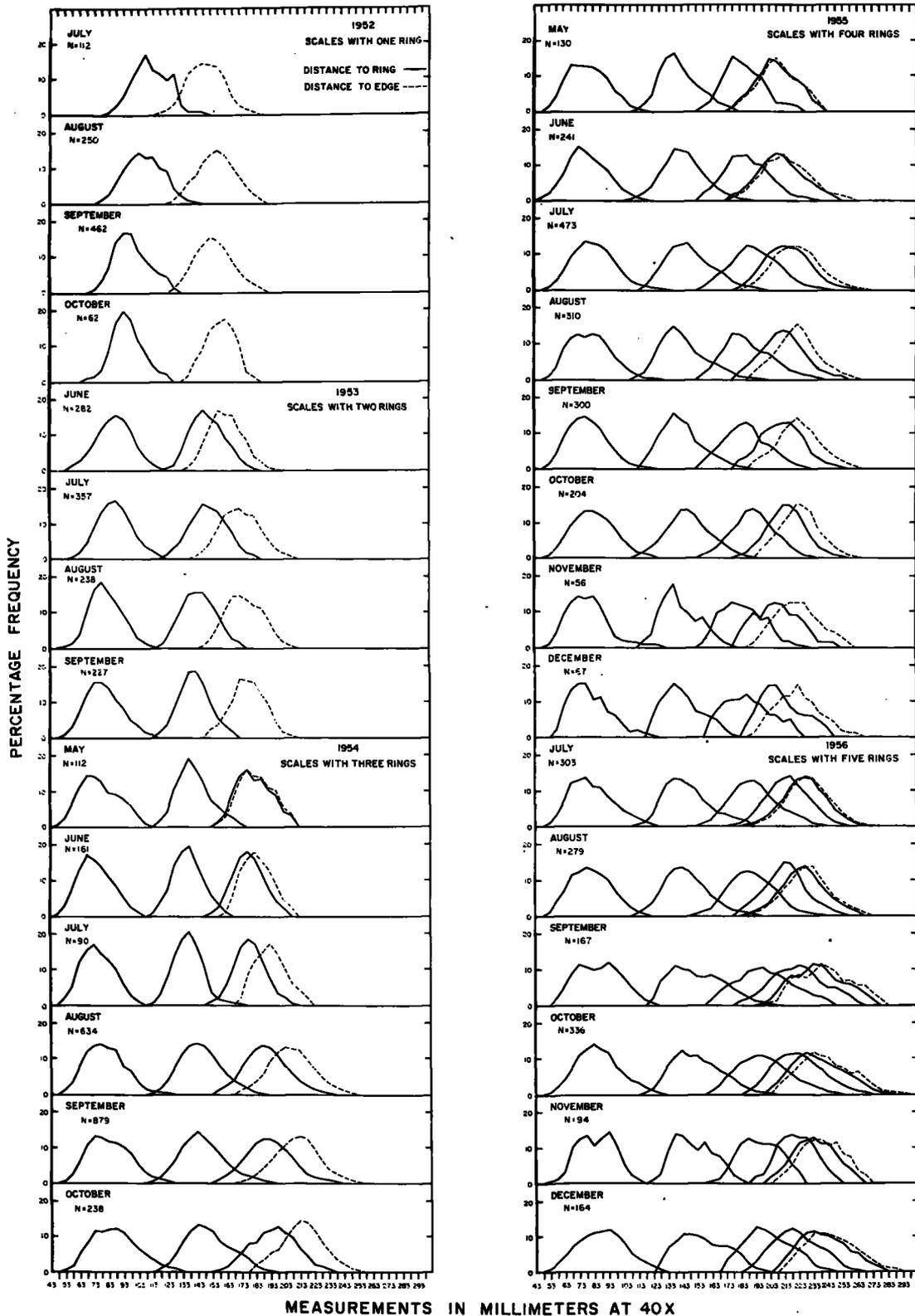


FIGURE 15.—Monthly frequency distributions of measurements of scale lengths to each ring and to the edge of the scale, 1951 ring class.

VALIDITY OF RINGS AS AGE INDICATORS

SCALE GROWTH

Evidence bearing on the validity of the scale method for determining the age of Atlantic menhaden is furnished by scale measurements, which were used to trace scale growth over a period of years. One method of establishing the validity of scale readings involves the reconstruction of the past growth history, based on either a real or assumed relation between body length and scale dimensions (Van Oosten 1929; Whitney and Carlander, 1956). In this study, however, we have used only the scale measurements. Our method yields the same results, but in terms of scale length rather than fish length. Scales arbitrarily assigned to ring-classes 1951 and 1952 were used for this purpose. Those which showed 1 ring in 1952 were designated as the 1951 ring class and those with 2 rings in 1954 were designated as the 1952 ring class. Growth of scales assigned to the 1951 ring class was followed over a period of 5 years (1952 through 1956) and of the 1952 ring class, over a period of 2 years (1954 and 1955).

Measurements of scales of the 1951 ring class which showed from 1 through 5 rings in successive years were plotted in 5-millimeter size classes as monthly frequency distributions, commencing with July 1952 (fig. 15). Absence of a commercial fishery during the winter months precluded adequate data during this period, hence, months represented by fewer than 50 fish were excluded.

Examination of figure 15 reveals several striking features in the curves, both within and between years. Most outstanding is the occurrence of one or more dominant, homologous modes in all of the monthly frequency distributions. Secondly, with the appearance of each additional ring on the scales, the mode of its frequency distribution is seen to persist in all subsequent months. However, there is an increase in the amount of overlap of the frequency curves representing each additional ring. Thirdly, the curves show an increase in the length of the scales with the addition of each new ring. Fourthly, the distance between the last two modes decreases in each successive year, and the distance from the last ring to the margin of the scale (dashed line) diminishes from year to year as each additional

ring appears on the scales. Fifthly, in each year the distance from the last submarginal ring to the edge of the scale increases through the summer months, reaching a maximum width in the fall. Finally, with the appearance of each new ring, the mode of its frequency distribution is seen to be homologous with that of the marginal increments in the latter months of the previous year, indicating that a new ring is laid down on the scale sometime between late winter and late spring.

Comparison of the combined monthly samples representing each ring group in successive years for the 5-year period (1952-56) is made in figure 16. Except for the first ring, the curves show a remarkably consistent pattern with respect to the location of each ring from year to year.

Scales assigned to the 1952 ring class first appeared in numbers in our samples as 2-ring scales in 1954. A plot of their measurements, as 2- and 3-ring scales in 1954 and 1955, respectively, is shown in figure 17. The curves show essentially the same features, both within and between years, as previously described for the 1951 ring class. In general, the modes of the frequency distributions representing the first and

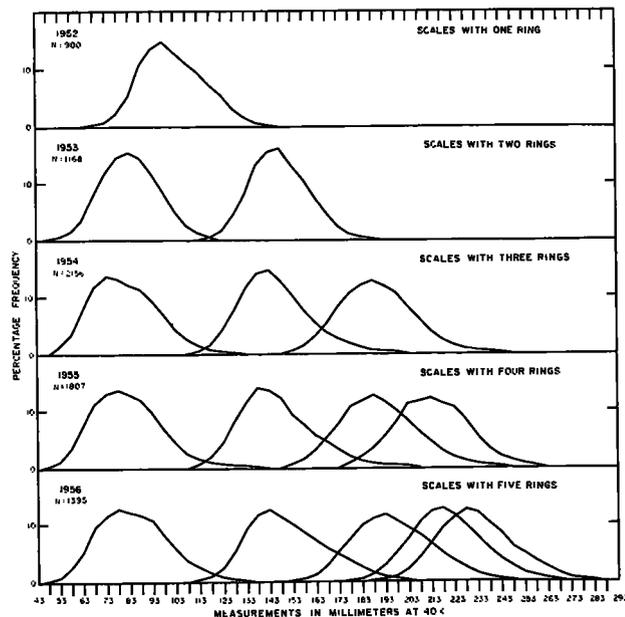


FIGURE 16.—Combined monthly frequency distributions of measurements of scale lengths to each ring, 1951 ring class.

second rings persist throughout; with the addition of the third ring, the mode of its frequency distribution persists thereafter; there is an increase in the length of the scales, both between months and between years; and the width of the submarginal zone increases during the summer in both years. The combined monthly data representing the 1952 ring class in each year (1954-55) are shown in figure 18. Again, the curves show a fairly consistent pattern between years in the location of the first two rings.

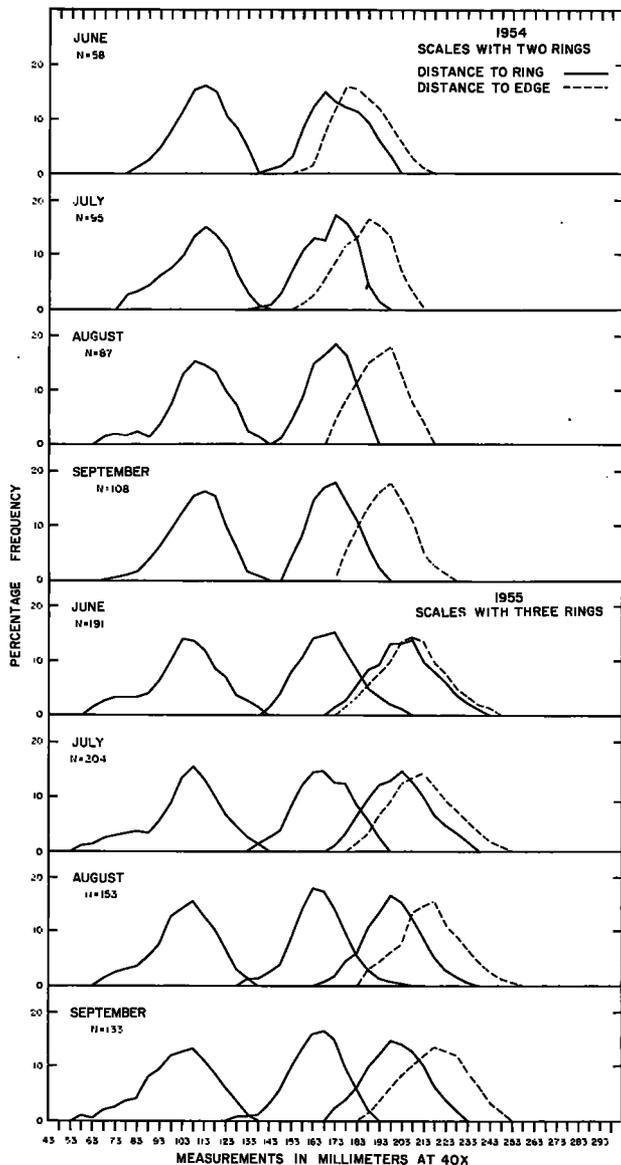


FIGURE 17.—Monthly frequency distributions of measurements of scale lengths to each ring and to the edge of the scale, 1952 ring class.

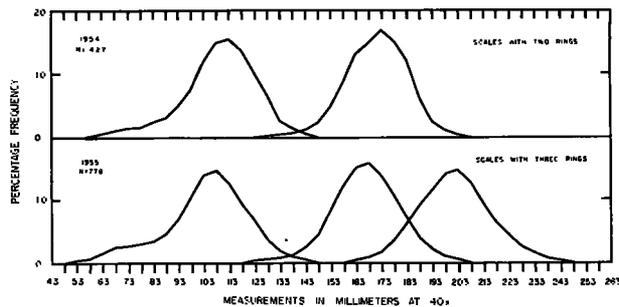


FIGURE 18.—Combined monthly frequency distributions of measurements of scale lengths to each ring, 1952 ring class.

DISCREPANCIES IN FREQUENCY CURVES OF SCALE GROWTH

While the foregoing discussion describes the general features of the frequency curves for each ring class, it is obvious that slight irregularities and discrepancies occur, both within and between each ring class. Chief among them is the failure within a ring class of homologous modes to occur in exactly the same position each month. This is particularly evident in the distance to the first ring. Frequencies of scale measurements to the first ring in the 1951 ring class (fig. 15) show a dominant mode at 108 millimeters in July which recedes to 93 millimeters in September and October. Comparison of the monthly means (table 1) indicated that these scales could not have been drawn from a homogeneous population as determined from measurements of the distance to the first ring ($F = 7.86$; $P 0.01 = \text{ca. } 3.80$). A further apparent decrease in the first year's scale growth may be seen in 1953 when the dominant mode receded from 88 millimeters in June to 78 millimeters in August and September. In subsequent years it shifted slightly in certain months, but remained relatively stable at about 73 millimeters. Furthermore, in 1953, when two rings were present on the scales, the mode of the frequency distributions representing the distance to the second ring appeared at 148 millimeters in June and July; however, by September it receded to 143 millimeters and thereafter continued to vary between 138 and 143 millimeters. Some variability also was evident in the frequency curves in subsequent years.

TABLE 1.—Frequencies of scale lengths (at 40 X) to the first ring of 1-ring fish sampled at Lewes, Del., and Wildwood, N.J., 1952

Size class	July	August	September	October
<i>mm</i>				
61-65.....			2	
66-70.....	1		2	
71-75.....		1	1	2
76-80.....		2	13	1
81-85.....	1	5	36	3
86-90.....	1	13	57	12
91-95.....	6	27	108	16
96-100.....	11	35	60	9
101-105.....	15	34	56	7
106-110.....	19	41	41	5
111-115.....	14	23	33	3
116-120.....	13	35	23	1
121-125.....	11	16	17	1
126-130.....	13	10	1	2
131-135.....	3	4	3	
136-140.....	1	2		
141-145.....	1	1		
146-150.....	1	1		
151-155.....	1			
Total.....	112	250	462	62
Mean.....	112.4	106.9	98.3	96.7

A slight downward shift in the location of the modes representing the first and second year's scale growth of the 1952 ring class also is evident over the period represented (fig. 17). In most months there is also a suggestion of a secondary mode at approximately 83 millimeters in the first year's scale growth.

Comparison of the modes representing the combined monthly samples for each ring class (figs. 16 and 18) shows that scales of the 1952 ring class exhibited a faster growth rate than those assigned to ring-class 1951. As 2-ring scales in 1954, the dominant mode of the first year's scale growth of the 1952 ring class is located at 113 millimeters and that of the second year's growth at roughly 173 millimeters. In contrast, the mode of the first year's scale growth for the 1951 ring class (of comparable age in 1952) is located at 83 millimeters and that of the second at 148 millimeters. Comparative growth of these two ring classes, as 3-ring scales, is demonstrated graphically in figure 19. Except for the slower growth exhibited by the 1951 ring class (solid line), the two curves are almost identical. These findings lend further confidence to the accuracy of our scale readings, for in addition to the number of rings present on the scales, those assigned to a given ring class exhibited a persistent growth pattern which distinguished them from an adjacent ring class.

Some of the discrepancies noted in the frequency curves may be attributable to the small numbers of fish represented in certain months.

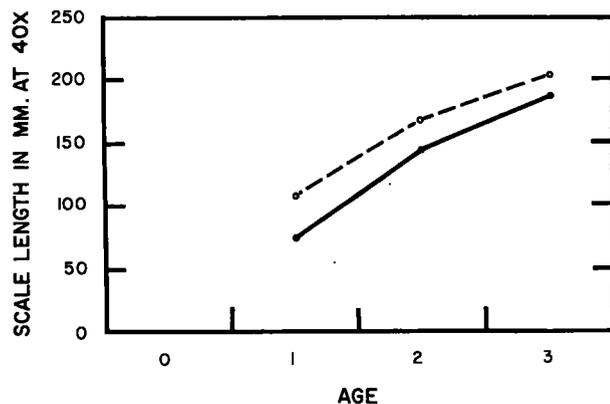


FIGURE 19.—Comparative growth rates of the 1951 (solid line) and 1952 (dashed line) ring classes as 3-ring scales.

A further source of bias lies in the fact that the bulk of our data were from fish selectively caught by purse seines. Hence, the observed progress of scale growth in successive months, and in successive years, may not have represented that of the population at large. Furthermore, comparisons between certain months were based on fish caught by purse seines and those taken by other gear and, therefore, may not have represented similar groups of fish.

Aside from these considerations, the variability in the position of homologous modes between months within each ring class is believed to be due largely to the movement of fish through a given locality during the fishing season. Based on the results of our coastwise sampling of the purse-seine catches over the past 3 years (1955 through 1957), the size of fish caught in a given locality, in general, was found to remain relatively constant or even to decrease throughout the summer; and the fish which contributed to the late summer fishery often were younger than those comprising the early summer fishery. Furthermore, fish of the same age caught in a given locality, in general, were found to be progressively smaller as the season advanced. An example is afforded from the summer catches landed at Beaufort, N.C., in 1955 (fig. 20). These findings would obtain only if the larger and older fish either were subject to a higher mortality rate, or emigrated and were continually being replaced by smaller and younger recruits. Before 1955 our sampling did not cover the range of any age group in the fishery and samples taken at the

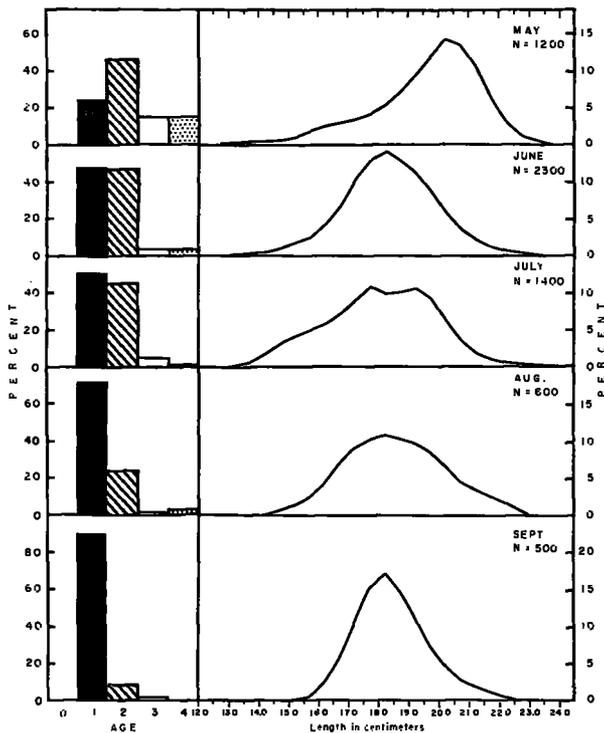


FIGURE 20.—Age and length composition of the summer purse-seine catch at Beaufort, N. C., 1955.

several locations were comprised of successively smaller fish as the season advanced. This was especially the case in 1952 and 1953 when most of our samples were obtained from purse-seine catches landed at Lewes, Del. When fish assigned to the 1951 ring class began to decline in the catches at Lewes in midsummer of 1954, sampling was extended northward to Port Monmouth, N.J., and Amagansett, N.Y., where this ring class dominated the catches.

The location of fishing also shifts frequently during the purse-seine season, depending on the availability of fish; hence, our samples may not have been truly representative of a given ring class over its entire range of distribution. As an example, the 1951 ring class was known to range from northern New Jersey to the northern Gulf of Maine during the summer of 1955. Although purse-seine fishing for Atlantic menhaden occurred no farther north than Casco Bay, Maine, that year, a few samples of this ring class were obtained from catches taken incidentally by weirs as far north as the Bay of Fundy. The northernmost fish of this group, therefore, were not well

represented in our summer samples. Also, fishing activities of the purse-seine fleet in southern New England waters shifted markedly throughout the 1955 season, ranging from Long Island Sound to Massachusetts Bay. Thus, when fishing concentrated for a time in Long Island Sound, larger fish of the 1951 ring class which occurred in Cape Cod waters may not have been well represented in our samples. Our data, therefore, cannot be assumed to represent completely the growth of the scales of fish of the 1951 ring class over its entire range.

A further apparent discrepancy noted in the curves was that a number of the distributions appear to be bimodal, especially those of the first year's scale growth in fish of the 1952 ring class. It might be that the two size groups suggested in the first year's scale growth represent fish belonging to different subpopulations (June 1958) or growth differences resulting from differential spawning.

MARGINAL SCALE GROWTH

Recognition of a newly formed age ring on the scales was based on the appearance of a narrow, clear band on the edge of the sculptured, anterior field. It is discernible earliest in the lateral areas adjacent to, and outside, a relatively wide, darker zone of regularly spaced ridges. It later becomes apparent anteriorly and, at this stage, may be traced around the entire sculptured portion of the scale.

To determine the time of year during which new rings formed on the scales, measurements of the projected scale image of the new growth zone, i.e., the distance from the last submarginal ring to the edge of the scale, were recorded when they approximated or exceeded 0.5 millimeter. Measurements of marginal increments were tabulated for each month for which data were available over a 5-year period, 1952 through 1956, for scales of the 1951 ring class and over a 2-year period, 1954 and 1955, for the 1952 ring class. Percentage frequency distributions of marginal increments, by 3-millimeter size classes, are shown in figure 21.

Scales assigned to ring-class 1951 were first obtained in late June 1952 (scales with 1 ring). It may be seen in figure 21 that they showed rather wide marginal growth zones which progressively increased in width through October.

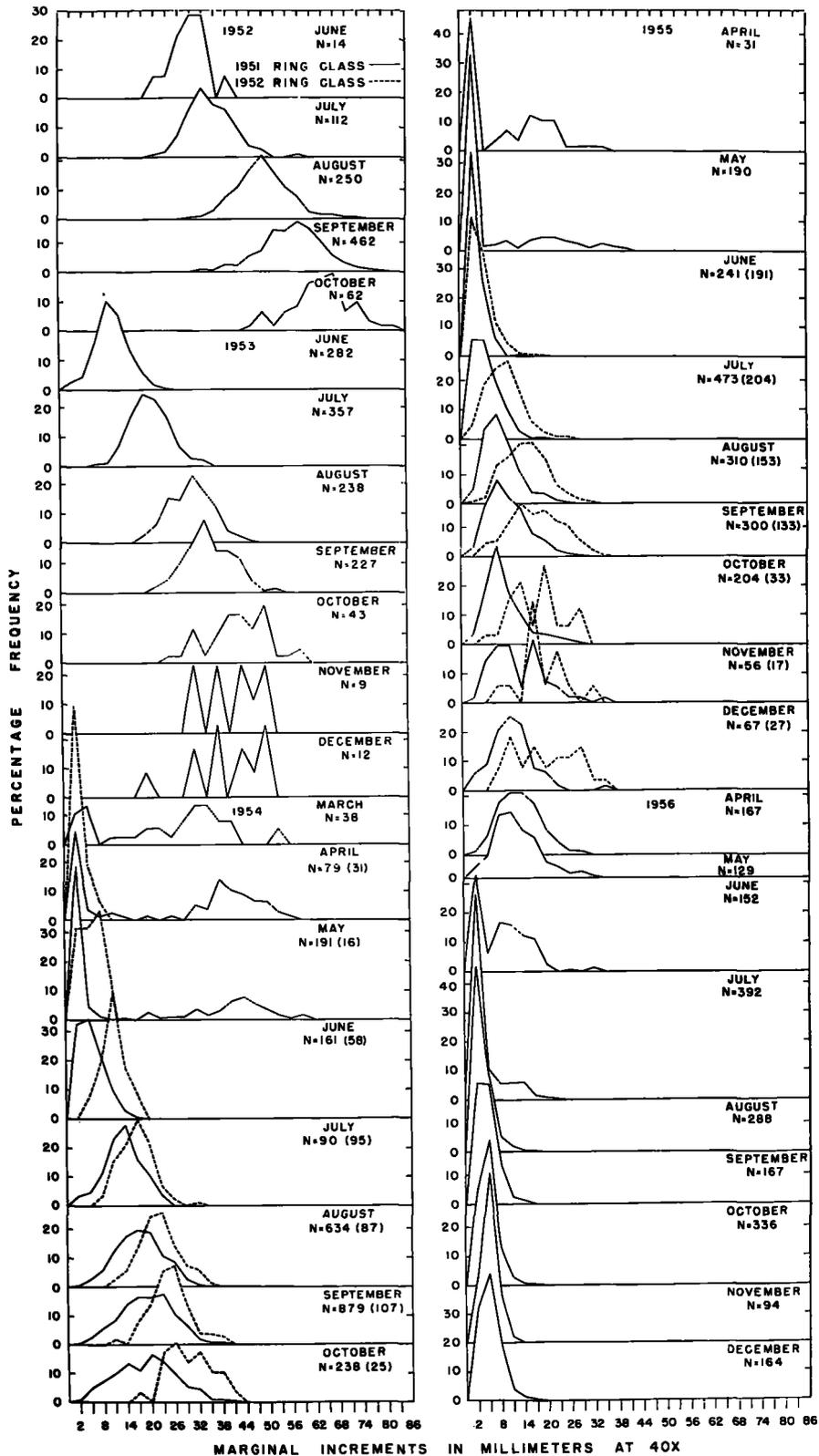


FIGURE 21.—Monthly frequency distributions of marginal increments of scales assigned to ring-classes 1951 and 1952.

In 1953, as 2-ring scales, the marginal zones were narrowest in June and again reached a maximum width in October. Of the scales collected in March, April, and May, 1954, some showed narrow marginal growth zones, but, in addition, scales with wide zones, evident the previous fall, also were present. In April and May the percentage of narrow margins increased, while the percentage of wide margins gradually diminished. By June only narrow marginal increments were evident, indicating that the third ring had formed on all scales, and it occurred at least 0.5 millimeter inside the margin. The new growth zones gradually increased in width as the summer progressed, reaching a maximum by September. An almost identical pattern of marginal growth is observed in 1955 when both narrow and wide growth zones were represented on the scales obtained in April. The percentage of narrow marginal growth zones again increased until June, and the modes of their frequency distributions advanced to a maximum in October. In April 1956 the mode of the frequency distribution was nearly identical with that of the previous December; it persisted through May, remained prominent in June, and was still evident in July. By August, however, only scales with narrow marginal growth zones were evident in the collections. This modal size class reached a maximum of only 5 millimeters by September, indicating that by the time the scales assigned to the 1951 ring class showed 5 rings, marginal scale growth was greatly reduced.

An attempt to follow similarly the growth of scales of this ring class through 1957 (as 6-ring scales) was abandoned when it was found that our grouping of marginal increments by 3-millimeter size classes was too large to show any prominent shift in modal size groups through the season. The average marginal growth by September amounted to only about 3 millimeters.

Except for a few scattered samples, scales assigned to ring-class 1952 first appeared in our collections in April 1954. At that time, they showed 2 rings with narrow marginal increments (shown by the dashed line in fig. 21). The new growth zone increased in width through the summer and reached a maximum in October. In 1955 the first scales of this ring class were ob-

tained in June. The marginal increments were narrowest at that time and gradually increased in width until October.

Although growth from the last submarginal ring to the edge of the scale occurred over an undetermined period of time before it could be measured and recorded, the foregoing findings show conclusively that (1) marginal scale growth was greatest during the warm months of the year, (2) the new ring was apparent earlier on the scales with fewer rings, and (3) formation of a ring occurred once each year and, therefore, must correspond in number with years of life. The data presented in figure 21 further indicate that the new ring was first evident on scales showing from 1 to 4 rings sometime between March and May and somewhat later on scales showing 5 rings.

The protracted period during which ring formation takes place, particularly in older fish, makes it difficult, or even impossible, to determine whether the marginal growth of the scale in some individuals represents a small, but complete, season's growth of the previous year, or exceptionally rapid growth made during the current season. The greatest difficulty, of course, occurs with scale samples obtained in May and June. It is of interest to note that scales of older fish (more than 5 rings) collected in 1955 and 1956 showed the appearance of a submarginal ring commencing in May, and in all age groups, ring formation was completed by late July. The tendency for apparently earlier ring formation in the younger age groups has been reported by other investigators (Hile 1941; Hodgson 1924); however, it must be recognized that scale growth is much slower in older fish, therefore, the new ring may not become visible until later in the season even though it may have been laid down at the same time as in previous years.

Because of the protracted period of ring formation in Atlantic menhaden, it becomes necessary in age analysis to choose some arbitrary date on which a fish is held to pass from one age group into the next. Based on the developmental stages of the gonads and the distribution of near-ripe fish in the catches, Higham (Ms.)¹ has demon-

¹ Joseph R. Higham. MS. Observations on the sexual maturation and spawning of Atlantic menhaden based on ova diameter measurements. Bureau of Commercial Fisheries Biological Laboratory, Beaufort, North Carolina. 1959.

strated that the bulk of spawning occurs from late fall until late spring. Accordingly, it seems reasonable to choose January 1 as the date of transition to the next higher age group. This practice requires that a virtual ring be credited to the edge of the scale from the beginning of the calendar year through the time of new ring formation. Ring classes, hereinafter referred to as year classes, therefore, may be designated according to the calendar year in which spring spawning takes place. Thus a fish caught in February 1955, showing 1 ring and a wide marginal growth zone on its scales would be designated as age 2 and assigned to year-class 1953; and since it could have been hatched any time between roughly November 1952 and June 1953, it may be from 20 to 27 months old at the time of capture.

This method of assigning fish to age groups and year classes has been incorporated into the routine age analysis of menhaden scale readings.

LOCAL DIFFERENCES IN MARGINAL SCALE GROWTH

To determine whether differences in the time of ring formation were indicated in various localities along the Atlantic coast, comparisons were made of marginal increments of scales from fish captured in May and June 1955 and assigned to the 1954, 1953, and 1952 year classes (1, 2, and 3 rings). Scale data are plotted in figure 22. Over the geographical range of each of these year classes represented in the commercial fishery, ring formation was completed sometime prior to May, except for a few individuals of the 1952 year class. Judging from the relative widths of the new growth zones, ring formation in each year class occurred earliest in southern waters and progressively later farther northward. Since the scales were read without knowledge of the locality from which they came, these findings support the conclusion that rings are not formed sporadically, but appear during the spring months. New scale growth varied considerably among individuals, especially in the younger age groups, and this variability is greatest in those fish occurring in southern coastal waters.

Since the menhaden purse-seine fishery commences at varying times and is dependent on different age groups in the different localities along the Atlantic coast, the foregoing findings

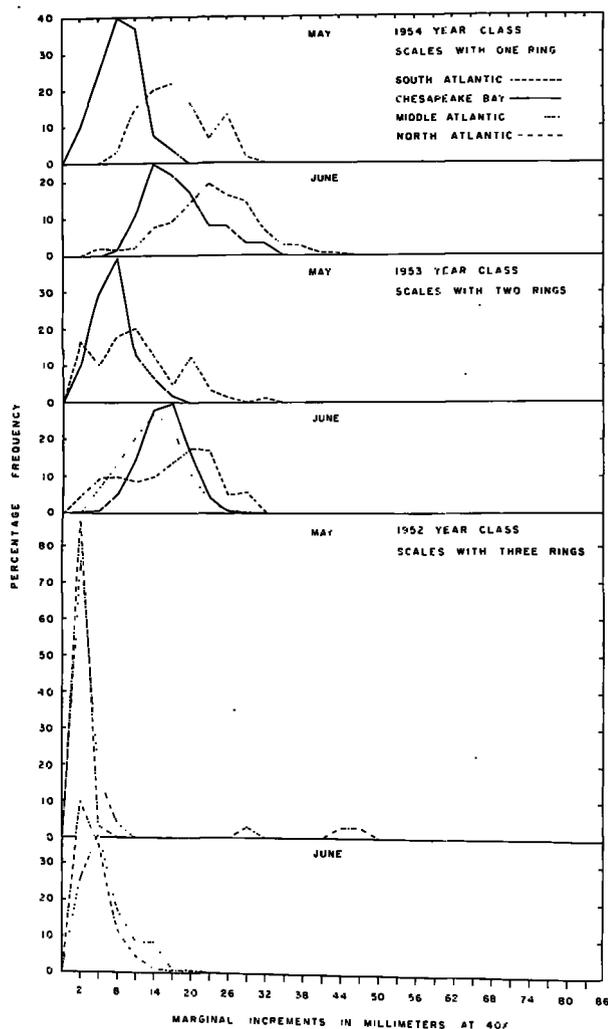


FIGURE 22.—Frequency distributions of marginal increments in scales from fish captured in 1955 and assigned to year-classes 1952 through 1954, from different localities along the Atlantic coast.

are of particular interest. Normally, the season in the southern waters (Beaufort, N.C., to Fernandina Beach, Fla.) begins about the first week in May and is based almost exclusively on the younger age groups, 1- and 2-ring fish predominantly. In Chesapeake Bay and middle Atlantic waters, the fishery normally gets under way during the last week in May. The Chesapeake Bay catch is comprised mostly of 1- and 2-ring fish, whereas 2- and 3-ring fish constitute the bulk of the middle Atlantic catch. In waters north of Long Island, fishing generally begins sometime in June and is based predominantly on older age groups.

The data presented in figure 22 indicate that ring formation in the first three age groups was completed at the onset of the 1955 purse-seine season in all localities. In older age groups, ring formation was completed in most individuals by the time the purse-seine fishery got under way in the northern waters in June. It was shown (p. 337 and fig. 21) that in 1955 the appearance of the new ring on scales of fish of the 1951 year class (4 rings) was completed in all individuals by June; however, by mid-May ring formation was completed in about 70 percent of the scales examined. Of the remaining fish with wide marginal zones on the scales in May, every individual showed the new ring forming, but since new growth was less than 0.5 millimeter of the projected scale image, it was not recorded in our measurements. In 1956 only a small percentage of the fish assigned to the 1951 year class had laid down a complete ring on scales in April and May as shown by the wide marginal growth zones (fig. 21). Although both narrow and wide increments were represented in our data in June and July, 56 percent of the scales examined in June and 86 percent of those in July showed the new ring completely formed. New scale growth was apparent on all scales examined in July, even though it was less than 0.5 millimeter on some of the scales and, therefore, was not recorded.

AGREEMENT IN PARALLEL READINGS

It was noted earlier (p. 324) that two independent readings were made on all scale samples in the collections. A tabulation of these results indicated a high percentage of agreement between the two readings in the different years, varying between 90.2 and 95.9 percent (table 2). The major portion of the disagreements for all years involved the first ring (51.3 percent). Differences

TABLE 3.—Number of disagreements in two independent readings of 1955 scale samples resolved in joint readings, according to number of rings

Number of rings	Number of scales examined	Original disagreements resolved in joint readings
0.....	422	7
1.....	923	34
2.....	2,934	80
3.....	1,999	113
4.....	3,543	165
5.....	654	146
6.....	229	42
7.....	64	10
8.....	15	1
9.....	5	1
10.....	2	2
Illegible.....	96
Total.....	10,886	601

in the interpretation of marginal growth on the scales accounted for a small percentage of the total (8.1 percent). The bulk of the remaining disagreements involved the location and number of rings (39.5 percent), and errors in measurements comprised about 1 percent of the disagreements.

A summary of the original disagreements, according to the number of rings, which were encountered in reading the 1955 scale samples and resolved in the joint readings, is presented in table 3. Application of a chi-square test to the data leads to the conclusion that the different age groups did not contribute equally to the disagreements ($\chi^2 = 50.26$; $P < 0.001$). Examination of the data indicated that the disagreements were proportionately higher in the older fish. Further consideration of the disagreements in the last five age groups indicated that more than 97 percent involved a choice of two adjacent rings, or uncertainty of the existence of only one of the rings. The remainder involved uncertainty as to the presence of more than one ring.

From the results of final disposition in the joint readings (last column, table 2), only a small

TABLE 2.—Agreement in age readings of Atlantic menhaden scales collected from 1952 through 1955

Year	Number of scales examined	Independent readings				Joint readings				Final disposition			
		Agreement		Disagreement		Agreement		Disagreement		Agreement		Illegible	
		Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
1952.....	1,602	1,575	94.8	27	5.2	67	77.0	20	23.0	1,642	98.8	20	1.2
1953.....	1,585	1,429	90.2	156	9.8	140	89.7	16	10.3	1,569	98.0	16	1.0
1954.....	4,222	4,050	95.9	172	4.1	80	46.5	92	53.5	4,130	97.8	92	2.2
1955.....	10,886	10,189	93.6	697	6.4	601	86.2	96	13.8	10,700	98.1	96	0.9

¹ Includes approximately two-thirds of the 1955 data.

percentage of the total number of scales in each year was rejected as illegible. The higher percentage in 1954 was due largely to the discarding of scales in which mold formation obscured the sculptured pattern in the central portion of the anterior field. In 1955, scales were stored in a dehumidified room, and loss of material from this cause was precluded.

Although the number of errors represented in the final determinations is difficult to measure, the high percentage of agreement in the two independent readings indicates that recognition of the number and location of the defined age rings must have been based on similar, objective criteria. To minimize reading errors, we routinely have continued the practice of two independent readings of all scale samples, followed by a joint reading of those scales on which there is disagreement.

SCALES FROM FISH OF KNOWN AGE

Final evidence of the validity of scale rings as age indicators in Atlantic menhaden is furnished from fish of the 1955 year class reared at the U.S. Fishery Laboratory, Beaufort, N.C. Material for this study was collected in the Neuse River, North Carolina, on July 15 and 22, 1955. The fish were obtained with a beach seine and transported in a live car to an outdoor rearing pond. About 500 individuals, ranging from 74 to 93 millimeters in length, were transplanted successfully. Natural food was introduced continuously into the rearing pond by means of a circulating system which pumped water from the adjacent sound. Heavy predation by wintering herring gulls resulted in a high mortality during December 1955 and January 1956, and by the end of the winter the original number had been reduced by more than one-half. The pond was drained and the remaining 64 fish were removed on September 27, 1956, after 14 months of confinement.

Samples of fish were preserved at the time of transplantation and periodically throughout the rearing period. Scales were removed from all preserved specimens and examined for growth characteristics. None of the scales showed any indication of ring formation before March 18,

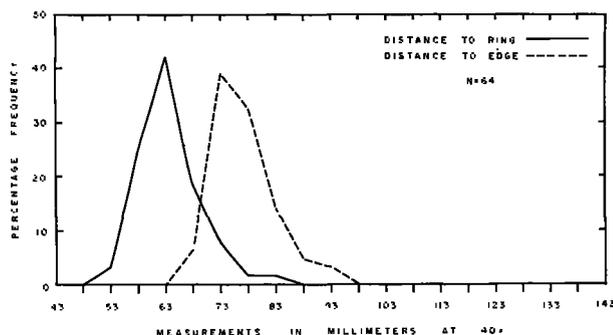


FIGURE 23.—Frequency distributions of scale measurements on 64 fish removed from a rearing pond at Beaufort, N. C., at the end of 14 months impoundment.

1956, when 20 of 54 specimens examined showed either a complete ring just inside the margin of the scale or traces of the new ring being formed in the lateral fields. On April 19 an additional 72 specimens were removed and all but 18 individuals showed a completely formed ring; however, an incomplete ring was discernible on all scales of the group. A sample was taken on May 2, and formation of the first ring on the scales had been completed in all specimens.

Scale measurements made on the 64 specimens removed at the end of the impoundment period are shown in figure 23. Without exception, only 1 ring was present on the scales. A single mode occurs in the length frequencies of the first year's scale growth, followed by a single mode in the curve representing scale growth in the second year of life.

These results show that only one ring was formed on the scales of Atlantic menhaden impounded over a 14-month period and that it is a reliable age mark. This experiment further demonstrated that the onset of ring formation on the scales varies among individuals, but is completed between March and May.

SUMMARY

1. Scales for ascertaining the validity of rings as age indicators were obtained from 13,510 juvenile and adult Atlantic menhaden taken in gill-, pound-, and fyke-net, purse-seine, and beach-seine catches. From 1952 through 1954, scale samples were obtained along the middle Atlantic coast of the United States. In 1955 scales were collected

over the range of the commercial fishery from Portland, Me., to Fernandina Beach, Fla.

2. Scales of menhaden may be differentiated from those of most other herringlike fishes by the serrate or pectinate posterior margin. The anterior field is sculptured with ridges running more or less parallel to the anterior margin.

3. Scales were examined and measurements made of the distances from the proximate center of the base of the sculptured field to each ring and to the margin of the scale with an Eberbach projector at a magnification of 40 X. All scales were read at least twice, and differences in the independent readings either were reconciled or the scales discarded.

4. Age rings were identified by the interruptions of the ridges in the sculptured field. Such areas of discontinuous ridges form light bands which are parallel to the margin and occur in the same relative position on all except regenerated or damaged scales of an individual fish.

5. The principal argument for the validity of rings as age indicators was based on scale measurements, which were used to trace the growth of the scales over a period of years. Measurements of scales from fish arbitrarily assigned to the 1951 and 1952 ring classes demonstrated the occurrence of one or more homologous, dominant modes in monthly frequency distributions. The data further showed that (a) each new ring on the scales persisted in the same relative position in which it appeared, (b) the scales increased in length with the number of rings, (c) the distance between the last two adjacent ring modes decreased with age, (d) the distance between the last submarginal ring and the margin of the scale increased through the warm months of the year, reaching a maximum in fall, and (e) the modes of the frequency distributions representing newly formed rings were homologous with those of marginal scale growth in the latter months of the previous year.

6. The major discrepancies in the frequency distributions of measurements of scale lengths were (a) failure within a ring class of homologous modes to occur in the same position each month, and (b) a downward shift of modes representing the first and second year's scale growth, both within and between years. These discrepancies

were ascribed primarily to inadequate sampling. Different growth rates were demonstrated in scales assigned to two different ring classes.

7. Based on the increase in width of the new growth zone (between the last submarginal ring and the edge of the scale), it was demonstrated that (a) new scale growth occurred during the warm months of the year, (b) a new ring is apparent earlier in younger fish, and (c) ring formation occurred only once each year, between March and May.

8. Differences in the amount of new scale growth were found in several geographical localities along the Atlantic coast. In general, ring formation was found to occur earliest in southern waters and progressively later farther northward.

9. Comparison of independent interpretation of scales by two readers showed a high percentage of agreement. Of the few disagreements, most involved the first ring. Disagreements were also higher among scales from fish in the older age groups.

10. A further verification of the validity of scale rings as a record of age was based on fish impounded over a period of 14 months. Results showed that only one ring appeared on the scales during this period, and it was formed sometime between March and May.

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SEASONAL ABUNDANCE AND VERTICAL MOVEMENTS OF PLANKTONIC CRUSTACEA IN LAKE MICHIGAN

By LARUE WELLS



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ABSTRACT

Plankton collections were made in Lake Michigan on seven occasions between June 6 and November 18, 1954, and 3 times between June 30 and October 2, 1955. The 1954 sampling area was about 8 miles off Grand Haven, Mich., at a depth of 74 meters, and the 1955 sampling was done about 3 miles offshore near Frankfort, Mich., at a depth of 46 meters. Limited sampling was also completed off Sturgeon Bay, Wis., on May 4, 1958. Collections were made with a Clarke-Bumpus plankton sampler with a net of No. 2 bolting silk. Series of samples were taken at about 2-hour intervals from 10-meter depth intervals from the surface to 40 meters (collections also from 5 meters in 1955).

Eight species of cladocerans (*Daphnia galeata mendotae*, *Daphnia retrocurva*, *Bosmina longirostris*, *Diaphanosoma brachyurum*, *Holopedium gibberum*, *Sida crystallina*, *Leptodora kindti*, *Polyphemus pediculus*), and 9 species of copepods (*Cyclops bicuspidatus*, *Mesocyclops edax*, *Diaptomus minutus*, *Diaptomus ashlandi*, *Diaptomus sicilis*, *Diaptomus oregonensis*, *Epischura lacustris*, *Limnocalanus macrurus*, *Senecella calanoides*), as well as the malacostracans *Pontoporeia affinis* and *Mysis relicta* were collected in numbers sufficient to permit individual treatment. In addition the cladocerans *Chydorus sphaericus*, *Eurycerus lamellatus* and *Ceriodaphnia* sp., and the copepods *Eucyclops prasinus* and *Cyclops vernalis* were taken in extremely small numbers. *Eurycerus lamellatus*, *Polyphemus pediculus*, *Cyclops vernalis*, and *Senecella calanoides* are reported for the first time from Lake Michigan.

Most species reached only one population peak a year. Apparently all cladocerans and the copepods *Mesocyclops edax* and *Epischura lacustris* overwinter as eggs in Lake Michigan.

All species migrated vertically to some degree. The vertical movements were influenced most strongly by diurnal changes in light intensity. Water temperatures also affected the migrations, especially of the cold-water forms. Migration toward the surface usually began late in the day. Most species attained their greatest numbers at the surface near sunset or soon afterwards. Numbers at the surface usually decreased toward midnight and, according to limited evidence, some species increased at the surface again between midnight and dawn. A few cold-water forms did not ordinarily migrate through a sharp metalimnion.

SEASONAL ABUNDANCE AND VERTICAL MOVEMENTS OF PLANKTONIC CRUSTACEA IN LAKE MICHIGAN

By LARUE WELLS, *Fishery Research Biologist*, BUREAU OF COMMERCIAL FISHERIES

Lack of knowledge concerning the plankton offers a major impediment to the development of a better understanding of the trophic relationships that govern the biological productivity of the Great Lakes. Opportunities for systematic investigation of plankton have been few. Research vessels have operated in the Great Lakes on a most limited scale and when available have been largely obligated to other aspects of fishery research. Furthermore, plankton research is difficult, often almost to the point of frustration. The inevitably biased sampling of presently available equipment and the characteristics of the plankton itself, the erratic horizontal distribution, pronounced diurnal and seasonal changes in vertical distribution, and seasonal changes of species composition and abundance combine to deprive the investigator of the precision he wishes to attain. These difficulties are not overcome easily or quickly. We can, nevertheless, make substantial advances if we recognize clearly the importance of even limited contributions to knowledge. We must seize every opportunity to obtain new information even though the individual studies may of necessity have many faults and weaknesses. The present report on observations made from the research vessel *Cisco* in Lake Michigan in 1954 and 1955 is restricted as to time, locality, and problems considered. It does, however, add measurably to our understanding of conditions in the lake and can aid greatly in the planning and execution of the more extensive researches that we trust will be possible at a later date.

Previous zooplankton studies on Lake Michigan have been few, and usually have been based on samples from inshore areas. Actually, nothing more than scanty works have been published on the limnetic crustacean plankton of any of the

upper Great Lakes. Ahlstrom (1936) excluded crustaceans from his study of plankton in deep-water samples from Lake Michigan. Among the earliest works on Lake Michigan zooplankton were a brief account of the daphnids in the Chicago water supply (Birge 1882) and a description of species in a few tow-net samples from Grand Traverse Bay, northeastern Lake Michigan, and southern Lake Michigan off Racine, Wisconsin, and Chicago (Forbes 1882). Birge (1894) found no cladocerans in samples taken in April from several locations in northern Lake Michigan. Marsh (1895) made rough estimates of the relative abundance of copepods in collections made during a limnological survey of Lake Michigan in the Grand Traverse Bay region in 1893. Details of the survey were discussed in Ward (1896). The most thorough study of Lake Michigan zooplankton to date has been an analysis of samples taken from inshore waters in southern Lake Michigan in 1887-88 and 1926-27 (Eddy 1927). Damann (1945) analyzed plankton collections taken from 32- to 38-foot depth off Chicago, but he did not identify zooplankters beyond genus.

The most important zooplankton studies in the other Great Lakes include those of Smith (1874), Forbes (1891), Birge (1893), and Eddy (1943), for Lake Superior; Sars (1915), and Bigelow (1922), for Georgian Bay (Bigelow included Lake Erie and the Lake Ontario data also); Wilson (1929), Chandler (1940), Andrews (1953), Davis (1954), and Tidd (1955), for Lake Erie. The previously listed reports by Birge (1894) and Marsh (1895) also contained information on zooplankton of Lake St. Clair. In other large bodies of water in North America, Langford (1938), and Rawson (1956) have made thorough plankton studies in Lake Nipissing and Great Slave Lake, respectively.

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Valuable suggestions concerning species identification and enumeration were made by David C. Chandler, Professor of Zoology, University of Michigan.

METHODS

COLLECTION OF SAMPLES

Ten series of day-and-night plankton collections were made in Lake Michigan in 1954 and 1955 from the U. S. Fish and Wildlife Service research vessel *Cisco*. In 1954, 7 series of samples were taken from June to November off Grand Haven, Michigan, and in 1955, 3 series were collected between June and October off Frankfort, Michigan. The collection area near Grand Haven was about 8 miles offshore at a depth of 74 meters, and the location near Frankfort was about 3 miles offshore at a depth of 46 meters. An additional single afternoon series was collected in May 1958 about 4 miles offshore at a depth of 33 meters off Sturgeon Bay, Wisconsin.

Collections were made with calibrated Clarke and Bumpus (1940) plankton samplers. Samples were taken in 1954 on June 6-7, 27-28, July 16-17, August 7, 27, October 7, and November 18; in 1955 on June 30, July 24, October 2; and in 1958 on May 4. Procedures varied from time to time, but on most dates samples from several levels were taken approximately every 2 hours from afternoon until near midnight; sampling continued until dawn on two occasions. Ordinarily each series of samples in 1954 consisted of 10-minute tows at the surface and at 10, 20, 30, and 40 meters. In 1955, a standard series included 5-minute tows at the surface and at 5, 10, 20, 30, and 40 meters. On June 6-7, 1954, nets were towed at only the surface and 10 meters. The single afternoon series on May 4, 1958, included samples from 5-minute tows at 2, 4, 8, 10, 15, and 20 meters.

The nets were made of No. 2 bolting silk (aperture 0.366 mm.) except for a few of the earlier tows on June 6, 1954, when No. 10 bolting silk (aperture 0.158 mm.) was used. The towing speed was approximately 4 miles per hour. At this speed an average of slightly more than 1,000 liters of water a minute passed through the samplers. The depths of the tows were controlled on the basis of calculations involving the length of cable below the surface and the angle between the surface and the cable.

All samples were preserved in 10-percent formalin and labeled with date, time, length of tow, depth of tow, mesh size, station number, and time at beginning of series. These records, as well as weather conditions and Clarke-Bumpus meter readings, were also kept on special forms. Bathythermograph tracings were made periodically and surface temperatures were recorded constantly during the collection periods. In the 1954 studies, water samples were taken from several depths with Nansen bottles preceding the collection of each 2-hour series of plankton samples. The water was analyzed for oxygen, pH, conductivity, and several other chemical characteristics.

COUNTING PROCEDURE

Vast differences in the size and numbers of the various species in the plankton required that counting procedures be varied. First, amphipods and mysids were removed from the samples and counted individually. Then all *Polyphemus* and *Leptodora* were enumerated, except that where the latter was very numerous only one-fourth of the sample was examined. For counting the remainder of the species, subsamples were removed from samples which had been diluted to either 50 cubic centimeters, 100 cc., or occasionally 200 cc., depending on the size of the sample. For most species, duplicate 5-cc. subsamples were taken; each sample consisted of 1.67-cc. portions taken with an automatic pipette from near the surface, center, and bottom of the container holding the thoroughly mixed sample. Only 0.5-cc. samples were employed to obtain counts of *Cyclops*, *Mesocyclops*, and *Diaptomus*, (duplicated for the former two), owing to the generally great abundance of these copepods. All organisms were identified to species except female and immature *Diaptomus*, which were combined to form a single category.

Counts were made under a binocular microscope at magnifications of 9× to 27×. Occasionally, higher magnification was necessary. Counts of the duplicate subsamples were averaged. Discrepancies between the two counts ordinarily were small although the percentage differences sometimes were high when a species was sparsely represented. When disagreement between the subsamples was so large that an error was considered likely, a third subsample was examined and the aberrant one disregarded. Most of the counts

given here are adjusted so that they are on a basis of organisms per cubic meter (1,000 liters) of water. A unit volume of 10 cubic meters (10,000 l.) was required, however, for *Senecella*, *Leptodora*, *Polyphemus*, *Pontoporeia*, and *Mysis* to prevent the use of fractions. All final calculated values above 100 have been rounded off to two significant figures. Values less than 100 were rounded to the nearest 10 organisms for those species for which only 0.5-cc. samples were examined.

LIMITATIONS OF THE DATA

Probably the outstanding weakness in the collection method is the use of comparatively large mesh in the nets. The No. 2 bolting silk unquestionably allowed the loss of valuable data. Many of the copepods in early developmental stages escaped, and adults of *Eucyclops prasinus* were probably poorly sampled. The conclusions concerning copepods therefore apply mainly to adults and the larger immature forms. All important cladocerans and malacostrans, except possibly *Bosmina longirostris*, are believed to have been adequately sampled in all size groups. Actually, the original plans called for the use of No. 10 mesh, but after the first few tows in 1954 it became obvious that the large amounts of algae caught would make the counts of crustaceans extremely difficult. Even in the No. 2 mesh enough filamentous diatoms were caught at times to make accurate subsampling and counting troublesome. On some occasions fine mesh could have been used without difficulty, but the larger mesh was used throughout so that samples would be comparable. Moreover, the large mesh is no doubt superior to the smaller in the filtration of water. It is believed that the No. 2 bolting silk was good in this respect, whereas smaller meshes probably would have varied, depending on whether or not algae had clogged the net.

A second weakness of the methods is the lack of samples near the bottom in 1954. The 1955 samples, however, were much better in this respect. It is doubtful whether many serious misinterpretations of the data resulted from the lack of the tows near the bottom in 1954, since counts from the 40-meter tows show that most species were scarce below 30 meters. There were, however, two or three cold-water forms which, no

doubt, were comparatively numerous near the bottom, at least in the daytime.

Objections are often raised to the use of horizontal tow nets for plankton collections because only certain levels are sampled and large concentrations of organisms may be missed. Vertical tows would have reduced the danger of missing crustaceans concentrated at certain levels, but would have been inferior in sampling organisms with uneven horizontal distribution. The nature of the horizontal distribution of zooplankton is still the subject of some argument, but the evidence for uneven distribution is strong (Marsh 1901, Southern and Gardiner, 1926, Wilson 1929, Cushing 1951).

The data on vertical migration would, of course, have been improved by 24-hour series of collections. The data do, however, show movements during the more important hours of the day, even though the material netted at daybreak is scanty. The discussion of migration will be concerned primarily with movements at twilight, but a fairly confident statement of movements at dawn can be made.

The lack of winter and early-spring samples permits only speculation on abundance during this period. The early-May collections are so few that they are useful only in determining the presence or absence of the various species at this time. Despite these shortcomings, an analysis of the population trends through the periods of collections permits estimates of abundance of many of the species during the winter.

HYDROGRAPHY OF SAMPLING AREAS

No attempt is made in this report to explore all possible factors affecting the vertical movements of crustacean plankton. It is clear from the data that change in light intensity was the dominant influence. It is equally evident that the water temperature had an effect on the movements of some species. Diurnal changes in dissolved oxygen, pH, and conductivity were so small that significant influence by these factors seems unlikely. Therefore, only diurnal changes in light intensity and the prevailing water temperatures are considered in the discussion of the vertical movements.

A certain amount of thermal stratification existed during each collection period except May

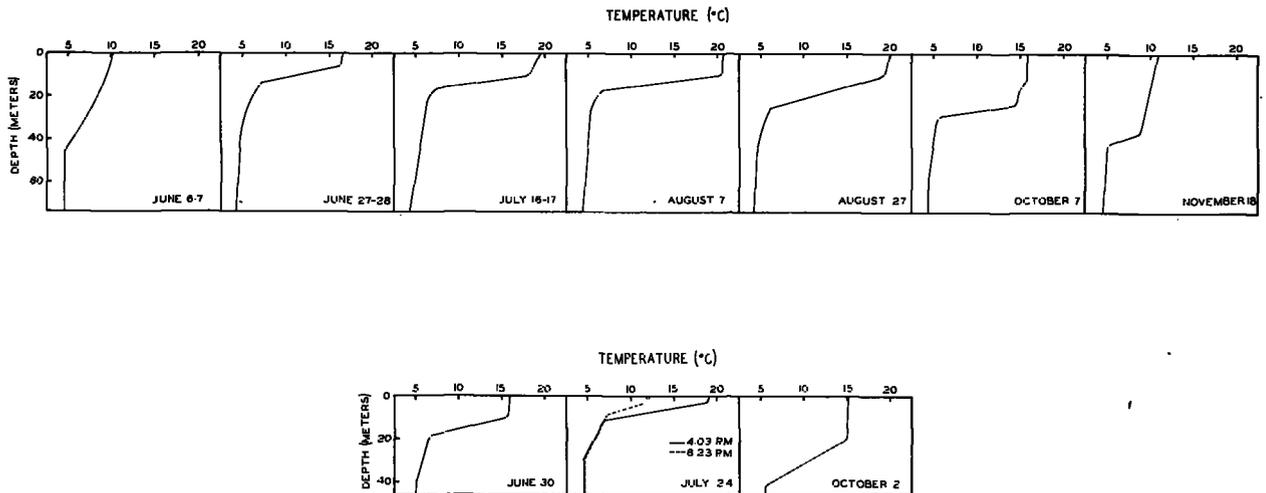


FIGURE 1.—Bathythermograph tracings for Lake Michigan in areas of plankton collections, 1954 (above) ; and 1955 (below).

1958 (water homothermous at about 4° C.), but the degree of stratification changed with the season (table 1, fig. 1). In 1954 the top of the metalimnion varied from near the surface to 10 meters below it, until the October and November collections when it was about 30 and 40 meters, respectively. Surface temperatures varied from 10.3° to 20.6° C. in 1954. In 1955 a most unusual thermal condition developed in the study area during the July sampling. An upwelling following strong north winds dropped the surface temperature from 18.9° C. at 4:03 p.m. to 11.7° C. at 8:23 p.m. (table 1, fig. 1), where it remained with little change during that study period. Limnological conditions in the area of upwelling probably resembled conditions usually confined to the

hypolimnion so that comparisons of plankton catches made on this date with catches of other dates might be misleading. Surface temperatures during the June and October collections in 1955 were 15.9° and 15.1° C., respectively. The metalimnion was shallow and well defined on the former date; it was deeper and its temperature gradient was less pronounced on the latter.

No transparency measurements were made at the time of the collections, but close estimates can be made from the Secchi-disc readings obtained in the collection areas a few days before each study, excepting July 1955 (table 1).

Times of sunset and sunrise, if they occurred during the hours of sampling, are listed in table 1 for the various collection dates. Nighttime illumi-

TABLE 1.—Hydrographic data and times of sunset and sunrise for dates on which plankton collections were made in Lake Michigan, 1954 and 1955.

[Time of sunrise given only when sampling still was in progress]

Date	Surface Temperature ($^{\circ}$ C.)	Metalimnion			Secchi disc (meters)	Sunset (EST)	Sunrise (EST)
		Position below surface (meters)	Temperature change ($^{\circ}$ C.)	Change of temperature per meter			
1954							
June 6-7.....	10.3	0-47	10.3-4.5	0.1	4.2	8:20	-----
June 26-27.....	16.8	6-14	18.7-7.3	1.2	6.1	8:25	5:10
July 16-17.....	19.5	10-17	18.4-7.2	1.6	5.8	8:15	5:15
August 7.....	20.6	10-18	20.5-6.6	1.7	9.1	8:00	-----
August 27.....	20.0	10-26	19.4-6.1	0.9	6.4	7:30	-----
October 7.....	15.9	24-30	14.5-5.6	1.5	3.6	5:30	-----
November 18.....	10.9	37-43	8.9-5.1	0.6	5.5	4:35	-----
1955							
June 30.....	15.9	12-19	15.7-6.6	1.3	8.2	8:25	-----
July 24.....	¹ 18.9	3-12	18.9-6.7	1.4	-----	8:15	-----
Do.....	² 11.7	3-9	11.7-7.2	0.7	-----	-----	-----
October 2.....	15.1	20-42	15.0-5.5	0.4	4.9	6:25	-----

¹ 4:03 p.m. ² 8:23 p.m.

nation was influenced by bright moonlight on July 16-17, 1954, and on June 30 and October 2, 1955.

SPECIES COLLECTED

Eight species of cladocerans and 9 of copepods, as well as the malacostracans *Pontoporeia affinis* (Lindström) and *Mysis relicta* Lovén were taken in sufficient numbers to permit individual treatment. The species of the first two groups are listed below:

CLADOCERA

Daphnia galeata mendotae Birge
Daphnia retrocurva Forbes
Bosmina longirostris (O. F. Müller)
Diaphanosoma brachyurum (Léveillé)
Holopedium gibberum Zaddach
Sida crystallina (O. F. Müller)
Leptodora kindti (Focke)
Polyphemus pediculus (L.)

COPEPODA

Cyclops bicuspidatus Claus
Mesocyclops edax (Forbes)
Diaptomus minutus Lilljeborg
Diaptomus ashlandi Marsh
Diaptomus sicilis Forbes
Diaptomus oregonensis Lilljeborg
Epischura lacustris Forbes
Limnocalanus macrurus Sars
Senecella calanoides Juday

The cladocerans *Chydorus sphaericus* (O. F. Müller), *Eurycerus lamellatus* (O. F. Müller), and *Ceriodaphnia* sp., and the copepods *Eucyclops prasinus* (Fischer) and *Cyclops vernalis* Fischer were collected in extremely small numbers. *Eurycerus lamellatus* and *Cyclops vernalis*, both found only off Frankfort, are reported from Lake Michigan for the first time.

In the discussions to follow little attention is paid to differences in species composition in the two areas of study, as the year-to-year variations in either area are not known, and may be considerable.

SEASONAL DISTRIBUTION AND VERTICAL MIGRATION OF SPECIES

CLADOCERA

Daphnia

The taxonomy of the genus *Daphnia* has long been discouragingly confusing and controversial. Brooks (1957) has presented a strong argument

for the "splitters" of this group, and his nomenclature is used here.

Daphnia was often the most conspicuous of the zooplankters; in some collections it constituted the bulk of the sample. Two species were represented, *D. galeata mendotae* and *D. retrocurva*. Both were considerably more abundant in 1954 than in 1955. In 1954 *retrocurva* was the more plentiful in late June and July and *galeata* during early June, October, and November; abundance was about equal in August. *D. galeata mendotae* was somewhat more numerous than *retrocurva* in practically all 1955 collections.

Daphnia galeata mendotae

In 1954 this species was rare in early June, somewhat more numerous by late June, considerably so by mid-July, and at a population peak in early August. Its abundance decreased through late August and early October and it was scarce in mid-November (table 2). In 1955, the species became more numerous on the successive collection dates, but never reached the abundance of 1954. It was absent in May 1958. Population trends indicate an absence of adults and juveniles in winter and early spring.

Comparisons of these findings with those of other workers are often difficult because the particular species to which they refer is not always evident. *Daphnia longispina*, a name which in recent years has been applied to most of the North American varieties of the genus except *D. magna*, *D. retrocurva*, and *D. pulex*, has been found in all the Great Lakes. Most of these Great Lakes records are probably based on either *D. galeata mendotae* or *D. dubia* of Brooks (1957). Brooks has, in fact, observed the former in Lake Ontario samples. In Lake Erie *D. longispina* has been reported to have a spring and fall pulse (Chandler 1940) and a fall maximum (Davis 1954). In a definite reference to *D. galeata mendotae*, the species was found to attain maxima in June and again in late August and early September in Pymatuning Reservoir on the Pennsylvania-Ohio border (Borecky 1956). Birge (1898) reported that *D. hyalina* Leydig (a synonym of *D. galeata mendotae*, according to Brooks 1957) had spring and fall maxima and a winter minimum, in Lake Mendota, Wisconsin.

TABLE 2.—*Daphnia galeata mendotae* per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1954						
June 6, 7:						
2:00 p.m.	0	-----	0	-----	-----	-----
4:00 p.m.	0	-----	3	-----	-----	-----
6:00 p.m.	0	-----	0	-----	-----	-----
8:40 p.m.	2	-----	5	-----	-----	-----
10:00 p.m.	7	-----	2	-----	-----	-----
12:00 p.m.	2	-----	2	-----	-----	-----
1:00 a.m.	0	-----	-----	-----	-----	-----
June 27, 28:						
10:00 p.m.	-----	-----	26	-----	-----	-----
12:00 p.m.	280	-----	13	12	7	-----
2:00 a.m.	540	-----	-----	9	-----	-----
4:00 a.m.	210	-----	470	9	180	-----
July 16, 17:						
7:00 p.m.	12	-----	23	35	16	14
9:00 p.m.	3,000	-----	180	29	89	66
11:00 p.m.	3,000	-----	1,400	100	52	49
1:00 a.m.	1,200	-----	1,900	65	43	49
3:00 a.m.	2,500	-----	2,900	100	100	54
4:30 a.m.	920	-----	1,000	45	15	37
August 7:						
5:30 p.m.	100	-----	2,500	400	100	130
7:45 p.m.	2,200	-----	4,000	180	84	83
9:30 p.m.	5,100	-----	2,600	160	67	160
11:00 p.m.	4,400	-----	1,100	120	96	150
August 27:						
5:45 p.m.	0	-----	1,100	160	31	-----
7:30 p.m.	1	-----	640	87	-----	19
9:00 p.m.	2,300	-----	30	21	58	23
11:00 p.m.	1,400	-----	29	43	-----	9
October 7:						
5:15 p.m.	61	-----	650	130	31	24
7:00 p.m.	740	-----	780	34	23	-----
9:15 p.m.	600	-----	620	40	19	15
November 18:						
4:30 p.m.	18	-----	29	6	5	5
6:00 p.m.	32	-----	13	3	4	-----
8:00 p.m.	81	-----	-----	-----	2	5
10:00 p.m.	19	-----	29	14	3	-----
1955						
June 30:						
6:00 p.m.	1	4	9	8	3	2
8:30 p.m.	2	26	19	6	1	2
11:30 p.m.	24	11	8	3	1	0
July 24:						
4:15 p.m.	8	870	8	25	7	3
6:15 p.m.	50	540	220	3	1	2
8:15 p.m.	59	18	12	3	-----	1
10:45 p.m.	57	11	6	0	0	0
October 2:						
2:00 p.m.	9	680	1,300	-----	-----	27
4:20 p.m.	27	1,100	1,500	530	49	6
6:30 p.m.	130	1,100	850	210	6	6
8:20 p.m.	290	1,100	910	110	6	9
10:30 p.m.	290	240	-----	-----	4	5

D. galeata mendotae was strongly partial to the upper strata. The young were generally nearer the surface than the adults. A similar distribution was observed for *D. hyalina* Leydig by Juday (1903) in Winona Lake, Indiana. In the present study *D. galeata mendotae* was never taken in large numbers below the metalimnion, although some, mostly large, were observed in the deepest samples. *D. galeata* was absent or scarce at the surface during the bright daylight hours, when the greatest numbers were usually taken at 10 meters. It moved to the surface in large numbers at dusk, however, and reached its maximum abundance there about 1½ hours after sunset. During the July 1954 study the maximum was observed in

successive surface samples taken 45 minutes and 2 hours 45 minutes after sunset, but a sample between these times probably would have contained a still larger number. Abundance declined around midnight or somewhat before, and increased again toward dawn. The latter fluctuation occurred on both of the occasions when surface samples were taken until daybreak (June 27–28 and July 16–17, 1954). On both occasions, however, the numbers at the surface had dropped off sharply by the time (an hour before sunrise) the last samples were taken. The same type of drop in surface abundance in the middle of the night was noted for *Daphnia longispina* in two Colorado mountain lakes (Pennak 1944).

Vertical movement below the metalimnion was limited except in the early August study of 1954, when the small numbers at 20 meters (metalimnion 10–18 meters) decreased in evening samples. Considerable movement upward from the metalimnion was evident, however, on July 16–17 and August 7, 1954. Numbers at 10 meters (metalimnion 10 to somewhat less than 20 meters) on these dates increased out of proportion to decreases below the metalimnion. A graphical representation of the changes in vertical distribution of this species on August 7, 1954, is presented in figure 2. During the July 16–17 study there must have been a daytime concentration between the surface and 10 meters to account for the prodigious increase at the surface before numbers changed greatly at 10 meters.

The young of *D. galeata mendotae* appeared to reach the surface before the adults, perhaps because they had not so far to move. This difference of behavior was especially noticeable on August 7, 1954, when the young made up the entire catch in the first surface collection (5:30 p.m.) and practically all in the second (7:45 p.m.), but the older ones had become numerous by the time of the third surface sample (9:30 p.m.).

Vertical movement of *D. hyalina* Leydig has been reported in several Wisconsin lakes (Juday 1904) but little was noted in Lake Mendota, Wisconsin (Birge 1895). Several accounts have been published of diurnal migrations of *D. longispina*, but since the exact variety is not usually known, they are not discussed here. Ordinarily the movements have been toward the surface at night, but

in one lake a curious migration of large- and medium-sized individuals to the surface in daytime was observed (Southern and Gardiner, 1932).

Daphnia galeata mendotae reproduces sexually in Lake Michigan in the fall. In 1954 a few females with ephippia in early stages of development were seen in the early October collections, and many of the females (perhaps 20 percent) bore ephippia, some completely developed, in the mid-November collections. This sexual stage may be somewhat unexpected, since Pennak (1953), stated that "... in limnetic populations in large lakes it is thought that [*Daphnia*] reproduction may be entirely parthenogenetic the year round, especially in *Daphnia longispina*." Clemens and Bigelow (1922), however, found many *Daphnia* ephippia in stomachs of ciscoes (*Leucichthys* spp.) taken from Lake Ontario in October and Lake Erie in November. The species of *Daphnia* bearing the ephippia was not stated, but it must have been *D. longispina*, at least in the Lake Ontario fish, since this form (*D. l.* variety *hyalina galeata*) was the only one observed in that collection.

Daphnia retrocurva

Daphnia retrocurva was absent in the early June 1954 samples, fairly common in late June, at a population peak in July and early August, still common in late August, less so in early October, and scarce in mid-November (table 3). In 1955 it was scarce in late June, uncommon in late July, and fairly common in early October. It was not present in May 1958. Thus the species is probably absent except as eggs through the winter and most of the spring. Eddy (1927) considered the form generally common from April to November in his southern Lake Michigan samples. Population maxima of *D. retrocurva* have been observed in Lake Erie at various times between May and October (Chandler 1940, Davis 1954) and the species has been reported absent December to April (Tidd 1955). It has been found in Lake Superior (Forbes 1891, Birge 1893, Brooks 1957), Lake Ontario (Bigelow 1922, Brooks 1957), Georgian Bay (Sars 1915, Bigelow 1922), and Lake St. Clair (Birge 1894).

The vertical distribution and movements of *D. retrocurva* were almost identical to those of *D. galeata mendotae*, except for a somewhat later maximum at the surface. The comparison of

TABLE 3.—*Daphnia retrocurva* per cubic meter of water off Grand Haven, Michigan, in 1954 and off Frankfort, Michigan, in 1955

[None taken June 6-7, 1954]

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1954						
June 27, 28:						
10:00 p.m.			30			
12:00 p.m.	1,000		19	6	7	
2:00 a.m.	880			7		
4:00 a.m.	590		380	11	18	
July 16, 17:						
7:00 p.m.	20		100	120	130	77
9:00 p.m.	5,400		370	70	220	150
11:00 p.m.	9,500		1,900	170	76	100
1:00 a.m.	3,000		1,500	150	53	85
3:00 a.m.	4,800		2,900	160	160	92
4:30 a.m.	2,200		3,300	130	64	94
August 7:						
5:30 p.m.	14		4,300	520	150	190
7:45 p.m.	960		3,900	280	100	86
9:30 p.m.	4,500		4,000	180	150	180
11:00 p.m.	6,600		860	150	77	170
August 27:						
5:45 p.m.	0		250	98	12	
7:30 p.m.	1		670	49		13
9:00 p.m.	2,200		15	17	25	14
11:00 p.m.	1,100		18	23		7
October 7:						
5:15 p.m.	9		210	7	4	3
7:00 p.m.	24		180	10	8	
9:15 p.m.	120		140	8	4	3
November 18:						
4:30 p.m.	0		2	0	(1)	1
6:00 p.m.	0		2	1	0	
8:00 p.m.	2				(1)	(1)
10:00 p.m.	2		0	0	1	
1955						
June 30:						
6:00 p.m.	0	0	0	1	0	0
8:30 p.m.	0	0	2	6	0	0
11:30 p.m.	5		5	0	0	0
July 24:						
4:15 p.m.	3	300	8	17	1	1
6:15 p.m.	5	69	81	0	1	0
8:15 p.m.	30	19	13	4		2
10:45 p.m.	11	11	6	0	0	0
October 2:						
2:00 p.m.	2	110	670			
4:20 p.m.	2	230	430	340	38	27
6:30 p.m.	65	280	270	270	26	3
8:20 p.m.	100	370	270	320	6	3
10:30 p.m.	160	130			3	2

¹ Calculated value less than 0.5.

data for *D. retrocurva* collected on August 7, 1954, with those for *D. galeata mendotae* (fig. 2) shows the similarities. *D. retrocurva*, especially the young, favored the upper layers. It avoided the surface in bright daylight, moved to the surface around and following sunset (the young more quickly than the older ones), and decreased at the surface during the middle of the night. On 1 of 2 occasions it increased in the early morning and declined again before sunrise. The evidence suggests some vertical movement as deep as 20 meters (just below the metalimnion) on August 7, 1954, and considerable migration up from a concentration in the metalimnion on July 16-17, 1954. Evidently many *D. retrocurva* concentrated between the surface and 10 meters on the latter date. They migrated up at night and caused a huge increase

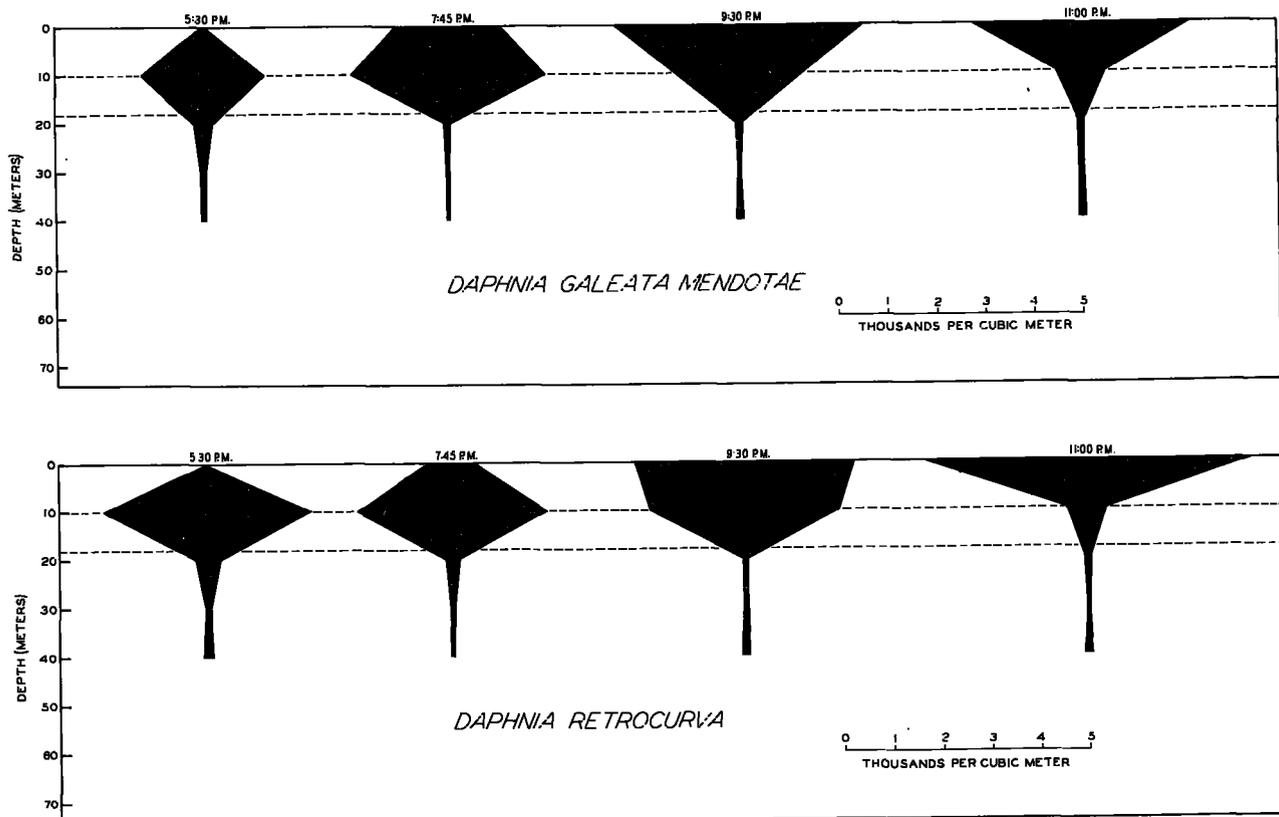


FIGURE 2.—Vertical distribution of *Daphnia galeata mendotae* and *D. retrocurva* on August 7, 1954 (time, Eastern standard; sunset 8:00 p.m.) The broken lines represent limits of the metalimnion. No samples were taken below 40 meters.

at the surface before any appreciable decrease appeared in the metalimnion. Several investigators have reported upward migration of *D. retrocurva* at night (Marsh 1898, Juday 1903 and 1904, and others).

No females bearing ephippia were observed.

Bosmina longirostris

Bosmina longirostris was present during all collection periods except May 1958, but usually was taken in small numbers (table 4). It is possible, however, that significant numbers of small individuals escaped through the No. 2 bolting silk. The species exhibited no striking changes in seasonal abundance, but their absence in May and small numbers in early June indicate that they carry over winter and early spring as eggs. Catches in late June and July of both years were sufficiently large to suggest an early-summer maximum, but differences are too small for definite conclusions. Eddy (1927) reported *B. longirostris*

to be rare in southern Lake Michigan but stated that *B. longispina* was the most abundant cladoceran. *B. longirostris* has been reported most common in Lake Erie at various times from May to December and rare or absent at other times (Chandler 1940, Davis 1954, Tidd 1955). It is also present in Lake Superior (Forbes 1891) and Georgian Bay (Sars 1915, Bigelow 1922).

The generally small numbers of individuals taken and the rather erratic changes at the various levels prevent detailed analysis of the vertical distribution and migration of *B. longirostris*. This species ordinarily occurred in greater numbers in the upper layers, and on several occasions, including all three collection dates of 1955, increased at the surface at night. None were at the surface in mid-afternoon in early June 1954 but thereafter numbers at this level increased steadily until midnight. The largest numbers were found at the surface in the first series of samples in July and October 1954, but on both occasions the col-

TABLE 4.—*Bosmina longirostris* per cubic meter of water off Grand Haven, Michigan, in 1954 and off Frankfort, Michigan, in 1955

Date and time	Surface	Depth in meters				
		5	10	20	30	40
<i>1954</i>						
June 6, 7:						
2:00 p.m.	0	0	0	0	0	0
4:00 p.m.	0	0	0	0	0	0
6:00 p.m.	2	0	0	0	0	0
8:40 p.m.	12	3	3	0	0	0
10:00 p.m.	20	5	5	0	0	0
12:00 p.m.	20	9	0	0	0	0
1:00 a.m.	1	0	0	0	0	0
June 27, 28:						
10:00 p.m.	0	66	0	0	0	0
12:00 p.m.	460	100	30	17	0	0
2:00 a.m.	420	10	0	0	0	0
4:00 a.m.	1,200	360	61	48	0	0
July 16, 17:						
7:00 p.m.	330	13	29	17	6	0
9:00 p.m.	37	21	110	17	9	0
11:00 p.m.	12	5	23	21	5	0
1:00 a.m.	5	15	19	20	3	0
3:00 a.m.	15	45	23	13	5	0
4:30 a.m.	79	68	11	6	4	0
August 7:						
5:30 p.m.	27	19	35	9	5	0
7:45 p.m.	26	31	20	34	3	0
9:30 p.m.	8	87	6	25	11	0
11:00 p.m.	31	110	10	8	8	0
August 27:						
5:45 p.m.	5	47	7	4	0	0
7:30 p.m.	18	37	13	0	2	0
9:00 p.m.	20	8	5	8	3	0
11:00 p.m.	11	29	5	0	4	0
October 7:						
5:15 p.m.	160	160	5	13	6	0
7:00 p.m.	59	130	21	6	0	0
9:15 p.m.	89	89	84	15	7	0
November 18:						
4:30 p.m.	33	24	9	2	3	0
6:00 p.m.	0	10	2	4	0	0
8:00 p.m.	16	0	0	8	5	0
10:00 p.m.	20	57	20	5	4	0
<i>1955</i>						
June 30:						
6:00 p.m.	25	34	52	14	5	0
8:30 p.m.	200	220	190	93	7	0
11:30 p.m.	320	90	300	14	1	0
July 24:						
4:15 p.m.	17	79	310	74	12	0
6:15 p.m.	56	92	310	13	1	0
8:15 p.m.	280	710	160	23	4	0
10:45 p.m.	160	1,100	300	55	3	0
October 2:						
2:00 p.m.	12	99	46	0	0	0
4:20 p.m.	39	86	65	110	14	0
6:30 p.m.	36	140	76	220	45	0
8:20 p.m.	37	120	100	140	2	0
10:30 p.m.	65	82	150	160	5	0

rise. Pennak (1944) observed only slight movement of this species in a Colorado lake. Juday (1904) reported movement of *Bosmina* to the surface at night in 3 of 7 Wisconsin lakes, but Marsh (1898) found that in Green Lake, Wisconsin, *Bosmina* was more common at the surface in the daytime than at night.

Diaphanosoma brachyurum

Small catches of *Diaphanosoma brachyurum* were made during every collection period except June 1955 (table 5) and May 1958. The species was rare during the studies of early June 1954 and July 1955, but the very small catches on the latter date may have been the result of the upwelling at that time. Although numbers are too small for definite conclusions regarding seasonal abundance, maxima appear to have occurred in early summer and fall of 1954 and fall of 1955. The absence in May 1958 and June 1955 and the scarcity in June 1954 indicate that the form is probably absent during winter and early spring. Eddy (1927) found this species during only September and October in southern Lake Michigan; it was commoner in the latter month. Most of the literature on seasonal abundance of *D. brachyurum* in the Great Lakes as well as smaller bodies of water points to a scarcity or absence during late fall, winter, and early spring, and a population peak in late summer or early fall (Chandler 1940, Davis 1954, Tidd 1955, Marsh 1898 and 1903, Birge 1898, Kofoid 1908, Scheffer and Robinson, 1939; Pennak 1949, Borecky 1956). This species has been reported also for Lake Superior (Birge 1893) and Georgian Bay (Bigelow 1922).

D. brachyurum favored the upper layers but was found at all depths. It increased at the surface at night on every occasion when appreciable numbers were taken. In late August 1954 it was not found at the surface until after sunset; on most other dates a few were at the surface before sunset. The species' preference for the upper strata and its movement to the surface at night in Lake Michigan is similar to its behavior in other lakes (Marsh 1898, Juday 1903 and 1904, Kikuchi 1930, Worthington 1931, Grover and Coker, 1940).

Holopedium gibberum

Holopedium gibberum was taken in July and October 1955, but was not abundant at either

lection time was near sunset. Surface collections earlier in the day probably would have yielded smaller catches. The species showed an increase in the two dawn surface samples (June 27-28 and July 16-17, 1954). These limited data indicate that this form usually migrated toward the surface late in the day, and after sinking during the middle of the night, probably moved up again briefly near dawn. Previous investigators have arrived at various conclusions as to the vertical migration of *Bosmina* (several authors have failed to designate the species). Kikuchi (1930) stated that in Japanese lakes *B. longirostris* had a confusing mode of migration and that most did not

TABLE 5.—*Diaphanosoma brachyurum* per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

[None taken June 30, 1955]

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1954						
June 6, 7:						
2:00 p.m.	0	0	0	0	0	0
4:00 p.m.	0	0	0	0	0	0
6:00 p.m.	0	0	0	0	0	0
8:40 p.m.	1	0	0	0	0	0
10:00 p.m.	0	0	0	0	0	0
12:00 p.m.	0	0	0	0	0	0
1:00 a.m.	0	0	0	0	0	0
June 27, 28:						
10:00 p.m.	0	0	0	0	0	0
12:00 p.m.	22	0	2	0	0	0
2:00 a.m.	11	0	0	0	0	0
4:00 a.m.	11	3	0	0	0	0
July 16, 17:						
7:00 p.m.	3	3	6	0	0	0
9:00 p.m.	15	2	2	2	0	0
11:00 p.m.	18	11	4	2	0	0
1:00 a.m.	7	9	2	5	2	0
3:00 a.m.	9	3	5	5	0	0
4:30 a.m.	3	3	0	1	0	0
August 7:						
5:30 p.m.	1	0	1	(¹)	0	0
7:45 p.m.	3	3	0	0	0	0
9:30 p.m.	3	9	0	(¹)	0	0
11:00 p.m.	3	3	2	0	2	0
August 27:						
5:45 p.m.	0	9	3	1	1	1
7:30 p.m.	0	25	2	1	1	1
9:00 p.m.	7	3	1	1	1	2
11:00 p.m.	8	1	1	1	1	2
October 7:						
5:15 p.m.	18	12	12	2	1	1
7:00 p.m.	38	31	27	8	8	2
9:15 p.m.	36	39	8	8	8	2
November 18:						
4:30 p.m.	2	10	4	0	1	1
6:00 p.m.	23	4	1	(¹)	0	0
8:00 p.m.	12	0	0	4	(¹)	0
10:00 p.m.	5	4	1	1	1	2
1955						
July 24:						
4:15 p.m.	1	1	1	0	0	0
6:15 p.m.	1	0	0	0	0	0
8:15 p.m.	1	0	0	1	0	0
10:45 p.m.	0	0	0	0	0	0
October 2:						
2:00 p.m.	2	29	21	10	4	4
4:20 p.m.	3	23	21	10	4	4
6:30 p.m.	11	34	19	21	10	3
8:20 p.m.	18	34	38	14	10	0
10:30 p.m.	19	32	34	51	0	2

¹ Calculated value less than 0.5.

time (table 6). Only two individuals were observed in the 1954 collections, both on August 27. Forbes (1882) found the species in Grand Traverse Bay; otherwise, it has not been previously reported for Lake Michigan. It has been found in Lake Superior (Forbes 1891, Birge 1893), Lake St. Clair (Birge 1894), Lake Erie (Bigelow 1922, Wilson 1929), and Georgian Bay (Sars 1915). It was described as very common only in the latter area.

The present data are not considered adequate to permit conclusions regarding the seasonal abundance of *Holopedium*, although there is evidence of absence in winter and spring and a fall maxi-

TABLE 6.—*Holopedium gibberum* per cubic meter of water off Frankfort, Mich., in 1955

[None taken June 30, 1955; none taken off Grand Haven, Mich., in 1954 except for two individuals on August 27]

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1955						
July 24:						
4:15 p.m.	2	4	0	0	0	0
6:15 p.m.	5	3	1	0	0	0
8:15 p.m.	4	0	0	0	0	0
10:45 p.m.	0	1	0	0	0	0
October 2:						
2:00 p.m.	5	22	10	5	0	0
4:20 p.m.	10	19	8	1	0	0
6:30 p.m.	24	12	14	1	0	0
8:20 p.m.	6	11	16	0	0	0
10:30 p.m.	6	4	12	2	0	0

mum. In Lake Nipissing, however, this species was found only in spring in two successive years (Langford 1938).

In Lake Michigan *Holopedium* was taken only in the upper 20 meters, or above the metalimnion. It was found in the daytime surface samples, but increased at the surface toward sunset. The peak occurred 2 hours before sunset in July, but at about sunset in October. In both months the peak was immediately followed by a decrease early in the evening. The October observations are thought to be the more dependable, since very few were taken in July.

Kikuchi (1930) stated that in Japanese lakes *Holopedium gibberum* moved up at night from the region of the thermocline or just above, reaching the surface in one lake but not in 2 others. Langford (1938) reported that in Lake Nipissing *Holopedium* was confined to the upper strata, but he did not discuss its vertical migration.

Sida crystallina

Sida crystallina was taken only in the October 1955 collections (table 7). It was present in most of the upper-level samples, but was not abundant in any of them. It is perhaps somewhat surprising that the species was found at all in such a limnetic habitat. Birge (in Ward and Whipple—1918) considered *Sida crystallina* as intermediate between littoral and limnetic forms and said that such species "... are never present in large numbers in the open water, nor are they likely to be found far out from the weedy margin." Southern and Gardiner (1926) found *Sida* occasionally in the littoral zone and stated that Apstein (1896) considered it a littoral species. Wilson (1929),

however, observed it in his "lacustric" zone (10-62 meters) in eastern Lake Erie. That the species was not taken in Lake Michigan in 1954 may be due to the greater distance of the collection area from shore. Most other workers have reported *Sida* from the shallow waters of the Great Lakes. The species usually has been reported as rare, although it was abundant in L'Anse Bay of Lake Superior (Forbes 1891) and in Lake St. Clair (Birge 1894).

Sida seems to be most abundant in the fall, as the present data would indicate. Southern and Gardiner (1926) stated that it reaches its maximum numbers in September and is absent during the winter. Eddy (1927) found it only in September and October, and then in very small numbers, in the inshore waters of southern Lake Michigan.

TABLE 7.—*Sida crystallina* per cubic meter of water off Frankfort, Mich. in 1955

[None taken June 30 and July 24, 1955, nor during any of the studies off Grand Haven, Mich., in 1954]

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1955						
October 2:						
2:00 p.m.	0	5	17			0
4:20 p.m.	0	4	8	5	0	0
6:30 p.m.	3	0	12	6	0	0
8:20 p.m.	9	2	0	4	0	0
10:30 p.m.	6	0	2	7	0	0

All *Sida* collected in the present study were in the upper 20 meters. This region was entirely in the epilimnion and had temperatures of 15.0°-15.1° C. The other levels sampled contained much colder water. No *Sida* were taken at the surface before sunset, but they were present in each of the three nighttime surface samples, and were most numerous about 2 hours after sunset. Numbers are too small for further conclusions regarding vertical migration.

Leptodora kindti

The large cladoceran *Leptodora kindti* was never taken in large numbers (table 8), but owing to its size it made up the bulk of a few of the samples. This species has been reported by nearly all investigators of Great Lakes zooplankton. It was absent in the early-June collection of 1954, but appeared in the late-June samples. It reached its peak of abundance in July and early August,

decreased somewhat in late August and had nearly disappeared by mid-November. In 1955 it was lacking in the late-June collections, and was apparently somewhat less numerous in July than in early October. It was not taken in May 1958. The data indicate an absence of *Leptodora* in Lake Michigan during winter and spring.

TABLE 8.—*Leptodora kindti* per 10 cubic meters of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

[None taken June 6-7, 1954 and June 30, 1955]

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1954						
June 27, 28:						
10:00 p.m.			19			
12:00 p.m.	489		27	1	12	
2:00 a.m.	374			1		
4:00 a.m.	170		193	7	7	
July 16, 17:						
7:00 p.m.	950		55	46	28	21
9:00 p.m.	182		286	157	37	19
11:00 p.m.	301		625	20	22	14
1:00 a.m.	45		241	30	6	11
3:00 a.m.	413		587	34	10	15
4:30 a.m.	41		562	34	16	12
August 7:						
5:30 p.m.	9		316	33	10	23
7:45 p.m.	890		499	27	23	28
9:30 p.m.	398	1,811	27	24	37	
11:00 p.m.	658		926	18	23	31
August 27:						
5:45 p.m.	10		146	14	5	
7:30 p.m.	46		123	71		6
9:00 p.m.	273		4	2	8	6
11:00 p.m.	219		8	4		4
October 7:						
5:15 p.m.	0		22	4	1	0
7:00 p.m.	10		20	0	2	
9:15 p.m.	19		35	2	1	1
November 18:						
4:30 p.m.	0		0	1	0	0
6:00 p.m.	8		2	0	0	0
8:00 p.m.	1		0	0	0	0
10:00 p.m.	0		0	0	0	0
1955						
July 24:						
4:15 p.m.	0	120	21	2	0	0
6:15 p.m.	16	82	32	0	2	2
8:15 p.m.	345	9	0	0		1
10:45 p.m.	160	10	4	2	0	0
October 2:						
2:00 p.m.	0	139	153			11
4:20 p.m.	1	197	181	128	34	0
6:30 p.m.	28	163	178	87	14	0
8:20 p.m.	173	200	189	120	10	2
10:30 p.m.	86	52	163	94	4	0

The present findings on the seasonal distribution of *Leptodora* generally agree with those of other workers. In Lake Michigan, Birge (1894) found none in April and Eddy (1927) reported it in only July and October. It is most common in Lake Erie in late spring, summer, and early fall (Chandler 1940, Davis 1954). The species is absent in smaller lakes from late fall to late spring, and is usually most abundant in late summer to early fall (Birge 1898, Southern and Gardiner, 1926, Marsh 1898 and 1903).

Leptodora was found at all levels in Lake Michigan, but was rather uncommon below the metalimnion. Except for July 1954 the only relatively large catches as deep as 20 meters were made in October 1955, when the epilimnion extended to this depth. Numbers increased at the surface at night, but the time of maximum numbers at the surface varied from more than 1 hour before sunset to nearly 2 hours after sunset. A few were at the surface 2½ hours before sunset in early August 1954. The data for July 1954 suggest a movement to the surface at dawn, but records of surface catches for that date vary so erratically that no safe conclusions may be drawn. No dawn rise was apparent in the June 1954 collections. The vertical movements of *Leptodora* appear to have taken place both in the epilimnion and metalimnion. There is good evidence that in late August 1954 many individuals moved to the surface from a depth greater than 20 meters (metalimnion 10–26 meters). The maximum number was not reached at 20 meters until sunset, after which most individuals disappeared from this level and at 10 meters while the numbers at the surface increased greatly.

Marsh (1901) stated that *Leptodora* appeared at the surface at almost exactly 45 minutes after sunset and left 45 minutes before sunrise, but other workers have not been so definite. Juday (1904) said that in Wisconsin lakes it appeared from shortly after to 1½ hours after sunset, and showed a wide variation in time of leaving. According to Southern and Gardiner (1932) its vertical movements vary from day to day, and some may migrate downward at night. Forbes (1891) found large numbers at the surface on a bright, sunny afternoon in Lake Michigan, Michigan. Thus it appears that vertical movements of *Leptodora* occur generally, but vary more than the movements of many other crustacean plankters.

Polyphemus pediculus

Polyphemus pediculus was taken only in the collections of late June, July, and early August 1954 and July 1955 (table 9). It was fairly numerous in July 1955, less so in early August 1954, and scarce otherwise. Southern and Gardiner (1926) who observed it in littoral swarms in Lough Derg and the River Shannon, stated that it was absent from November through April.

The species has not been previously reported for Lake Michigan, probably owing to its relatively small numbers and short duration of occurrence. It has been found, however, in Lake Superior (Forbes 1891, Birge 1893), Lake Ontario (Pritchard 1931), and is common in Georgian Bay (Sars 1915, Bigelow 1922).

TABLE 9.—*Polyphemus pediculus* per 10 cubic meters of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

[None taken June 6–7, Aug. 27, Oct. 10, and Nov. 18, 1954, and June 30 and Oct. 2, 1955]

Date and time	Surface	Depth in meters				
		5	10	20	30	40
<i>1954</i>						
June 27, 28:						
10:00 p.m.			1			
12:00 p.m.	9		0	0	0	
2:00 a.m.	19			1		
4:00 a.m.	28		1	0	1	
July 16, 17:						
7:00 p.m.	77		1	0	0	0
9:00 p.m.	3		0	0	0	0
11:00 p.m.	1		1	0	0	1
1:00 a.m.	0		0	0	0	0
3:00 a.m.	0		0	0	1	0
4:30 a.m.	0		0	0	0	0
August 7:						
5:30 p.m.	16		3	2	0	0
7:45 p.m.	87		54	0	3	1
9:30 p.m.	17		179	1	0	1
11:00 p.m.	17		13	2	1	3
<i>1955</i>						
July 24:						
4:15 p.m.	416	126	8	0	40	1
6:15 p.m.	913	209	74	3	0	0
8:15 p.m.	1,159	127	21	8		0
10:45 p.m.	517	101	41	54	1	0

Polyphemus definitely favored the upper strata in Lake Michigan, although it was present in some of the samples from 40 meters. Some individuals were counted in all the afternoon samples, but the figures point to a movement to the surface at dusk and dawn such as was described for Japanese lakes by Kikuchi (1930). The meager data, of course, render the statement regarding the dawn movement somewhat tenuous. It seems nearly certain, however, that numbers decrease at the surface immediately following a peak at about sunset or slightly before. In late June 1954 *Polyphemus* increased at the surface from midnight to dawn, but in July of that year none were at the surface after midnight. The very bright moonlight on the latter collection date might have had a strong influence, however.

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Cyclops bicuspidatus

Cyclops bicuspidatus was present on all collection dates and occurred in practically every sam-

ple (table 10). It was abundant in June and July 1954, decreased in August, was least common in early October, and had increased moderately by mid-November. In 1955 the form was abundant in late June and July but had declined considerably by early October. It was abundant in the May 1958 samples. Thus the evidence is convincing that *C. bicuspidatus* is more numerous in Lake Michigan in spring and early summer than in late summer and fall. A lack of winter samples prohibits further conclusions regarding seasonal abundance.

Eddy (1927) reported *C. bicuspidatus* common in southern Lake Michigan in April (his earliest sampling date) and May, but lacking in June. It was common to abundant from July to September, rare in October, common again in November, and absent in December. These findings are similar to those of the present study, except for the June data. Lake Erie workers have observed a spring maximum and generally low abundance the remainder of the year (Chandler 1940, Andrews 1953, Davis 1954, Tidd 1955). In smaller bodies of water *C. bicuspidatus* usually has been found to be uncommon in summer (Marsh 1903, Kofoid 1908, Plew and Pennak, 1949). Pennak (1949) described an exception, however, in one Colorado mountain lake which had an indefinite summer maximum. A summer scarcity existed in the shallow ends of Lake Washington (Scheffer and Robinson, 1939).

C. bicuspidatus generally preferred the upper 20 meters, but fairly large numbers occasionally were found at 30 and 40 meters. The species migrated to the surface at night; good evidence exists of some movement even at the 40-meter level. There appeared to be some movement through the metalimnion. Surface samples contained maximum numbers only 45 minutes after sunset on two occasions, but the numbers in surface samples were usually largest in the last sample taken, as late as 4 hours after sunset. *C. bicuspidatus* exhibited little vertical movement in Winona Lake, Indiana (Juday 1903) and in Colorado mountain lakes (Pennak 1944), but it ascended at night in Lake Mendota, Wisconsin (Birge 1895), in Caroga Lake, New York (Maloney and Tressler, 1942), and in Merom Gravel Pit Lake, Indiana (Plew and Pennak, 1949). In the latter lake it migrated during all

TABLE 10.—*Cyclops bicuspidatus* per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1954						
June 6, 7:						
2:00 p.m.	0		1,400			
4:00 p.m.	20		1,200			
6:00 p.m.	80		1,500			
8:40 p.m.	1,900		750			
10:50 p.m.	2,500		790			
12:00 p.m.	1,700		600			
1:00 a.m.	300					
June 27, 28:						
10:00 p.m.			1,100			
12:00 p.m.	1,200		480	420	80	
2:00 a.m.	850			280		
4:00 a.m.	680		1,400	310	190	
July 16, 17:						
7:00 p.m.	1,200		730	750	480	170
9:00 p.m.	3,200		1,300	990	570	260
11:00 p.m.	1,600		780	510	240	110 ¹
1:00 a.m.	690		790	490	290	110
3:00 a.m.	720		740	370	160	110
4:30 a.m.	340		2,200	360	180	170
August 7:						
5:30 p.m.	0		870	380	250	150
7:45 p.m.	80		280	190	140	50
9:30 p.m.	100		380	100	100	60
11:00 p.m.	150		2,400	90	90	50
August 27:						
5:45 p.m.	(¹)		150	300	100	
7:30 p.m.	30		600	200		20
9:00 p.m.	130		530	200	100	60
11:00 p.m.	310		700	60		80
October 7:						
5:15 p.m.	0		60	30	0	20
7:00 p.m.	10		60	30	10	
9:15 p.m.	30		50	20	10	0
November 18:						
4:30 p.m.	180		130	80	20	0
6:00 p.m.	550		150	40	10	
8:00 p.m.	250				20	10
10:00 p.m.	270		80	20	20	
1955						
June 30:						
6:00 p.m.	140	250	600	2,200	1,100	280
8:30 p.m.	870	380	440	1,600	250	190
11:30 p.m.	970	3,000	580	370	150	160
July 24:						
4:15 p.m.	0	820	1,600	680	310	140
6:15 p.m.	30	290	1,500	220	60	70
8:15 p.m.	170	470	290	60		90
10:45 p.m.	1,600	490	180	130	50	10
October 2:						
2:00 p.m.	10	90	350			
4:20 p.m.	10	110	70	110	40	80
6:30 p.m.	30	240	90	180	70	30
8:20 p.m.	60	200	240	90	30	0
10:30 p.m.	220	60			20	10

¹ Calculated value less than 0.5.

seasons, but the vertical range was small during the warm months.

Mesocyclops edax

In this report *Mesocyclops edax* and *M. leuckarti* are treated as distinct species, as suggested by Coker (1943). Because *edax*, according to Coker, is much more common and widespread than *leuckarti*, it is probable that the *M. leuckarti* of North American literature is usually the same form as *M. edax* of this report. Comparisons with the findings of other workers are made on this assumption.

No striking changes took place in the abundance of *M. edax* in 1954 from late June to early October (table 11). During most of this period the species was perhaps slightly less plentiful than *Cyclops bicuspidatus*, but in early October it was the more numerous of the two. In mid-November, however, *M. edax* was rare and in early June it was absent. It was not taken in May 1958. Thus *M. edax* is probably absent except in the egg stage in winter and early spring. It was common in the June and October 1955 collections, but rare in those of July. In view of the 1954 data, however, the reality of July scarcity seems questionable. The small catches well may have

TABLE 11.—*Mesocyclops edax* per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

[None taken June 6-7, 1954]

Date and time	Surface	Depths in meters				
		5	10	20	30	40
1954						
June 27, 28:						
10:00 p.m.			0		(¹)	
12:00 p.m.	920		10	20		
2:00 a.m.	690			0		
4:00 a.m.	630		500	50	40	
July 16, 17:						
7:00 p.m.	1,200		0	0	10	0
9:00 p.m.	500		100	20	20	0
11:00 p.m.	2,100		100	50	50	20
1:00 a.m.	2,060		410	50	0	10
3:00 a.m.	720		320	0	40	10
4:30 a.m.	270		60	20	10	0
August 7:						
5:30 p.m.	120		30	50	20	70
7:45 p.m.	780		1,000	20	10	10
9:30 p.m.	310		580	50	20	10
11:00 p.m.	550		270	50	10	10
August 27:						
5:45 p.m.	20		150	10	10	
7:30 p.m.	180		110	0		10
9:00 p.m.	1,300		0	20	0	20
11:00 p.m.	510		70	10		20
October 7:						
5:15 p.m.	30		140	30	50	30
7:00 p.m.	90		280	20	30	
9:15 p.m.	330		440	30	40	40
November 18:						
4:30 p.m.	0		0	0	0	0
6:00 p.m.	0		0	10	0	
8:00 p.m.	20				0	(¹)
10:00 p.m.	90		0	0	0	
1955						
June 30:						
6:00 p.m.	110	410	300	40	0	0
8:30 p.m.	180	410	200	10	30	0
11:30 p.m.	190	520	340	80	0	0
July 24:						
4:15 p.m.	20	70	0	0	0	0
6:15 p.m.	0	50	0	0	0	0
8:15 p.m.	40	0	0	0	0	0
10:45 p.m.	30	0	0	0	0	0
October 2:						
2:00 p.m.	0	110	340			
4:20 p.m.	0	180	40	290	40	40
6:30 p.m.	80	380	280	220	20	20
8:20 p.m.	230	340	460	80	30	10
10:30 p.m.	330	270			20	30

¹ Calculated value less than 0.5.

been a result of the upwelling in which the study was conducted. The scarcity of this species in the upwelled water might have been a result of its avoidance of cold water.

Other workers also have found *M. edax* to be a warm-season species. In the various Lake Erie studies it has been reported most common from June to September (Chandler 1940), late August to early September (Andrews 1953), May to October (Davis 1954), and June to August (Tidd 1955). Both Andrews and Tidd reported it lacking from December until mid-spring. The same summer maxima and winter scarcities have been described for several smaller bodies of water (Birge 1898, Marsh 1903, Kofoid 1908). In the Great Lakes other than Lake Erie, *M. edax* has been reported as common in Lakes St. Clair and Michigan (Marsh 1895) and Georgian Bay (Sars 1915). Eddy (1927) did not take it in southern Lake Michigan. The species apparently has not been reported for Lake Superior.¹

M. edax was more nearly restricted to the upper strata than was *Cyclops bicuspidatus*. Not many *edax* were taken below the metalimnion, even though most series contained a few even at 40 meters. Numbers at the surface increased markedly at night, except during the late June 1955 study. Migration up from the metalimnion took place in July and early August 1954, but there was no evidence of movement in the hypolimnion. The data on time of maximum abundance at the surface are inconclusive, due to the variability. *M. leuckarti* [*edax*] was an active vertical migrant in Lake Mendota (Birge 1895) and was assumed to behave similarly in Lake Erie (Wilson 1929). Juday (1903) reported little increase at the surface at night in Winona Lake, Indiana.

Eucyclops prasinus

Only a single *Eucyclops prasinus* was observed in all collections. Since, however, Eddy (1927) found the species common to abundant in southern Lake Michigan and Marsh (1909) stated that it was common in all of the Great Lakes, it seems likely that many individuals of this minute cope-

¹ Forbes (1891) in his report on Lake Superior Entomostraca, listed *Cyclops edax*, but stated in his text, "This *Cyclops* was taken in moderate numbers from Lake Michigan only." Davis (1954) apparently misinterpreted the listing (an understandable mistake in view of the title of the paper) and erroneously credited Forbes with having found the species in Lake Superior.

pod escaped through the meshes of the No. 2 bolting silk. Fortunately several samples taken with No. 10 bolting silk at 5 meters near the 1955 sampling area were available for examination. One each of these collections had been made in May, June, August, September, and November, 1955. *E. prasinus* was present in all but the May sample, and was most numerous, although not abundant, in the September collection. It appeared to be much less plentiful than either *Cyclops bicuspidatus* or *Mesocyclops edax*, but the evidence for this conclusion is of course limited.

Diaptomus

The abundant genus *Diaptomus* was represented by the species *minutus*, *sicilis*, *ashlandi*, and *oregonensis*. Only the mature males were enumerated separately. Females and copepodites of all species were combined in the counts. The same species were reported for Lake Michigan by Marsh (1895) and all but *D. oregonensis* were found by Eddy (1927). All four are also present in Lake Erie (Wilson 1929, Chandler 1940, Davis 1954, and Tidd 1955), and in Lake St. Clair (Birge 1894). Forbes (1891) stated that *D. sicilis* was the most abundant entomostracan in Lake Superior, and Eddy (1943) reported this species as among the most numerous copepods in the same lake. Sars (1915) found *D. oregonensis* abundant and *D. minutus* less so in Georgian Bay.

In the following treatment of the individual species, the discussion, of course, refers to mature males only, although most findings probably apply to mature females as well. Because only a small portion of each sample was examined for diaptomids, final figures for mature males are for the most part based on the observation of relatively few individuals. For this reason the figures vary somewhat erratically. Despite this weakness, however, the data reveal certain obvious features of seasonal abundance and vertical distribution. The comparisons with results of other investigators may not always be completely valid, since some workers may have included copepodites as well as adults in their observations.

Diaptomus minutus

The adult males of this species were most numerous in late June, and did not decline sharply until late August (table 12). They were entirely

absent in October 1955, and nearly so in October 1954, but in 1954 they reappeared in considerable numbers in November. They were present in the May 1958 samples. Findings of other workers differ appreciably, but generally *D. minutus* has been reported to have maximum abundance in summer. Eddy (1927) found *D. minutus* common in southern Lake Michigan from July to November in one year and in all months of collection (May, July, October) of another year. Chandler (1940) found the species in Lake Erie from June to September only. Tidd (1955) reported it present in Erie throughout the year but most plentiful in summer, and Davis (1954) found the maximum abundance in April, May, and July. It was scarce in Lake Nipissing in May, but the abundance rose

TABLE 12.—*Diaptomus minutus* (adult males) per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

[None taken October 2, 1955]

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1954						
June 6, 7:						
2:00 p.m.	0		100			
4:00 p.m.	0		30			
6:00 p.m.	30		30			
8:40 p.m.	60		60			
10:00 p.m.	200		130			
12:00 p.m.	220		60			
1:00 a.m.	250					
June 27, 28:						
10:00 p.m.			0			
12:00 p.m.	910		10	0	10	
2:00 a.m.	600			40		
4:00 a.m.	670		90	20	40	
July 16, 17:						
7:00 p.m.	750		10	30	10	0
9:00 p.m.	70		0	0	20	0
11:00 p.m.	200		30	20	20	0
1:00 a.m.	270		50	0	0	0
3:00 a.m.	210		100	20	0	0
4:30 a.m.	90		0	40	10	0
August 7:						
5:30 p.m.	30		30	50	0	20
7:45 p.m.	140		30	0	0	0
9:30 p.m.	40		90	0	0	0
11:00 p.m.	310		40	0	0	0
August 27:						
5:45 p.m.	10		0	20	0	
7:30 p.m.	40		0	0		0
9:00 p.m.	40		0	0	0	0
11:00 p.m.	70		20	0		0
October 7:						
5:15 p.m.	0		20	0	0	0
7:00 p.m.	0		0	0	0	0
9:15 p.m.	0		0	0	0	0
November 18:						
4:30 p.m.	80		90	60	60	60
6:00 p.m.	480		90	70	120	
8:00 p.m.	90				160	20
10:00 p.m.	50		170	140	60	
1955						
June 30:						
6:00 p.m.	180	410	80	0	70	20
8:30 p.m.	710	240	120	30	0	40
11:30 p.m.	180	200	0	30	0	0
July 24:						
4:15 p.m.	0	150	0	0	0	0
6:15 p.m.	110	180	60	0	0	0
8:15 p.m.	180	40	50	0	0	0
10:45 p.m.	150	0	0	110	0	0

rapidly in June to a maximum in July and August (Langford 1938).

Adult males of *D. minutus* strongly favored the upper layers. They were taken in appreciable numbers in deeper water only in November 1954, when the metalimnion was deep and poorly developed. The number at the surface increased definitely at night. On two occasions *D. minutus* was absent at the surface in the afternoon but it later appeared there in number. The time of maximum abundance at the surface, however, does not bear a consistent relation with time of sunset. Langford (1938) also found this form concentrated in the upper layers of Lake Nipissing, where its diurnal movements were complex. Movement to the surface at night did not always occur and when it did the sexes behaved differently. Marsh (1898) observed no evidence of vertical migration in Green Lake, Wisconsin. In Caroga Lake, New York, adults were concentrated below the thermocline, and showed a slight vertical movement (Maloney and Tressler, 1942).

Diaptomus sicilis

The relatively large numbers of adult males of this form in early June and mid-November 1954 suggests that it is the predominant species during the cold months. The mature males were fairly common in early June 1954, less so in late June and July, rare in early August, absent in late August, moderately represented in early October, and most abundant in November (table 13). The catches in 1955 were similar to those of the corresponding dates of 1954. The species was present in the May 1958 collections. Eddy (1927) found the species only occasionally in southern Lake Michigan in June, August, and September of one year, and not at all in another. Davis (1954) reported *D. sicilis* from Lake Erie throughout the year, but Tidd (1955) found it lacking in September–December.

Mature males of *D. sicilis* preferred the upper layers, but avoided the surface in bright daylight. After sunset, however, they were often most numerous at the surface. References to the vertical migration of this species are few. Wilson (1929) stated only that it does not migrate as actively in Lake Erie as *D. ashlandi*, and Marsh (1898) observed no evidence of vertical migration in Green Lake, Wisconsin.

TABLE 13.—*Diaptomus sicilis* (adult males) per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

[None taken August 27, 1954]

Date and time	Surface	Depth in meters				
		5	10	20	30	40
<i>1954</i>						
June 6, 7:						
2:00 p.m.	0		0			
4:00 p.m.	0		0			
6:00 p.m.	10		0			
8:40 p.m.	500		60			
10:00 p.m.	920		30			
12:00 p.m.	400		0			
1:00 a.m.	410					
June 27, 28:						
10:00 p.m.			130			
12:00 p.m.	180		10	0	20	
2:00 a.m.	210			40		
4:00 a.m.	110		30	60	0	
July 16, 17:						
7:00 p.m.	20		90	0	0	0
9:00 p.m.	130		10	0	10	0
11:00 p.m.	0		20	80	0	0
1:00 a.m.	0		20	0	0	0
3:00 a.m.	70		30	20	0	0
4:30 a.m.	0		30	40	0	0
August 7:						
5:30 p.m.	0		0	0	0	0
7:45 p.m.	0		0	0	0	0
9:30 p.m.	0		0	0	0	0
11:00 p.m.	50		0	0	0	0
October 7:						
5:15 p.m.	0		40	60	10	10
7:00 p.m.	0		40	60	10	
9:15 p.m.	50		100	20	0	0
November 18:						
4:30 p.m.	90		1,100	540	120	80
6:00 p.m.	2,800		1,500	200	110	
8:00 p.m.	1,500				30	90
10:00 p.m.	2,500		540	450	80	
<i>1955</i>						
June 30:						
6:00 p.m.	30	90	50	80	60	30
8:30 p.m.	120	0	0	60	60	0
11:30 p.m.	0	30	0	30	0	30
July 24:						
4:15 p.m.	0	40	100	290	0	10
6:15 p.m.	0	50	30	130	0	0
8:15 p.m.	50	80	100	80	0	0
10:45 p.m.	110	80	90	160	30	0
October 2:						
2:00 p.m.	0	0	0			
4:20 p.m.	0	0	0	30	0	0
6:30 p.m.	50	50	50	0	0	0
8:20 p.m.	0	0	0	0	0	0
10:30 p.m.	60	0			0	0

Diaptomus ashlandi

Adult males of this species were taken on all collection dates, and they were the most numerous of the diaptomids in the July collections of both years. The population was relatively low in early June, but increased rapidly in late June and continued abundant in July and early August (table 14). Numbers had declined by late August, and *ashlandi* was scarce in early October of both years. By mid-November, however, the abundance had regained the summer levels. Definite maxima of adult males occurred, therefore, in early summer and late fall. Other Great Lakes investigators have generally agreed on a peak of abundance in the summer, but not in the fall. Eddy (1927) reported this species most plentiful in Lake

Michigan in July in his 1926-27 samples (collection made also in May and October), but did not find it in his 1887-88 samples. Chandler (1940) observed *D. ashlandi* in nearly all of his Lake Erie samples and reported a May-September maximum; Davis (1954) observed maxima in January and June-July; and Tidd (1955) failed to take them in September-December. The peak abundance of this species in Lake Washington, reached in April and May, was followed by a near-disappearance in July and a small pulse in October (Scheffer and Robinson, 1939).

Adult males of *D. ashlandi* favored the upper layers, but during the summer of 1954 did not avoid the lower levels as much as did the other

TABLE 14.—*Diaptomus ashlandi* (adult males) per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

Date and time	Surface	Depth in meters				
		5	10	20	30	40
<i>1954</i>						
June 6, 7:						
2:00 p.m.	0		20			
4:00 p.m.	0		0			
6:00 p.m.	0		30			
8:40 p.m.	0		60			
10:00 p.m.	0		60			
12:00 a.m.	20		80			
1:00 a.m.	0					
June 27, 28:						
10:00 p.m.			90			
12:00 p.m.	700		60	40	20	
2:00 a.m.	460			20		
4:00 a.m.	40		240	60	40	
July 16, 17:						
7:00 p.m.	20		0	60	10	0
9:00 p.m.	230		190	50	80	50
11:00 p.m.	1,600		340	70	70	30
1:00 a.m.	340		170	80	50	60
3:00 a.m.	380		390	60	70	30
4:30 a.m.	20		320	90	10	0
August 7:						
5:30 p.m.	0		170	0	20	40
7:45 p.m.	310		520	30	40	0
9:30 p.m.	460		260	0	30	20
11:00 p.m.	670		80	30	10	30
August 27:						
5:45 p.m.	0		40	0	0	0
7:30 p.m.	20		110	0	0	0
9:00 p.m.	290		0	0	0	0
11:00 p.m.	150		60	50		10
October 7:						
5:15 p.m.	0		0	0	0	0
7:00 p.m.	20		0	0	0	0
9:15 p.m.	0		50	0	0	0
November 18:						
4:30 p.m.	90		980	100	50	10
6:00 p.m.	380		970	70	40	0
8:00 p.m.	270				20	20
10:00 p.m.	930		280	210	20	
<i>1955</i>						
June 30:						
6:00 p.m.	0		0	160	80	60
8:30 p.m.	90		110	70	60	30
11:30 p.m.	220		80	110	60	0
July 24:						
4:15 p.m.	0		150	210	0	0
6:15 p.m.	0		230	250	0	20
8:15 p.m.	0		120	50	0	0
10:45 p.m.	370		80	40	40	0
October 2:						
2:00 p.m.	0		30	0		
4:20 p.m.	0		0	0	0	0
6:30 p.m.	0		50	0	0	0
8:20 p.m.	0		0	0	0	0
10:30 p.m.	60		50			0

TABLE 15.—*Diaptomus oregonensis* (adult males) per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

Date and time	Surface	Depth in meters				
		5	10	20	30	40
<i>1954</i>						
June 6, 7:						
2:00 p.m.	0		0			
4:00 p.m.	0		0			
6:00 p.m.	0		0			
8:40 p.m.	100		0			
10:00 p.m.	0		0			
12:00 p.m.	0		20			
1:00 a.m.	40					
June 27, 28:						
10:00 p.m.			0			
12:00 p.m.	40		0	0	0	
2:00 a.m.	40			0		
4:00 a.m.	80		30	0	0	
July 16, 17:						
7:00 p.m.	20		230	90	10	0
9:00 p.m.	780		30	0	10	0
11:00 p.m.	30		30	0	0	0
1:00 a.m.	30		50	0	0	0
3:00 a.m.	70		60	0	0	0
4:30 a.m.	0		0	20	0	0
August 7:						
5:30 p.m.	0		0	0	0	0
7:30 p.m.	30		180	0	0	0
7:45 p.m.	40		670	0	10	20
9:30 p.m.	40		190	20	0	30
11:00 p.m.	70					
August 27:						
5:45 p.m.	0		150	40	20	
7:30 p.m.	0		0	50		0
9:00 p.m.	20		0	0	0	10
11:00 p.m.	290		0	50		10
October 7:						
5:15 p.m.	0		40	0	10	0
7:00 p.m.	40		40	0	0	0
9:15 p.m.	30		50	0	0	0
November 18:						
4:30 p.m.	80		850	140	140	0
6:00 p.m.	1,100		1,100	70	120	
8:00 p.m.	1,600				30	140
10:00 p.m.	1,400		660	190	40	
<i>1955</i>						
June 30:						
6:00 p.m.	0		130	110	0	0
8:30 p.m.	0		0	30	0	0
11:30 p.m.	0		50	110	0	0
July 24:						
4:15 p.m.	0		150	0	100	0
6:15 p.m.	0		280	0	0	0
8:15 p.m.	20		0	0	0	0
10:45 p.m.	70		80	40	0	0
October 2:						
2:00 p.m.	10		20	110		
4:20 p.m.	10		50	60	0	0
6:30 p.m.	0		50	90	0	0
8:20 p.m.	0		20	50	0	0
10:30 p.m.	60		50		0	0

diaptomid males. They were usually absent from the surface in bright daylight, but were often most abundant there at night. For some unknown reason, however, few migrated to the surface in early June 1954. Wilson's (1929) daytime samples from eastern Lake Erie indicated that *D. ashlandi* was mostly near the bottom in deeper water and near the surface in shallower water. He concluded that the species was an active diurnal migrant in the "lacustric" zone, but not in the littoral area.

Diaptomus oregonensis

The adult males of this species were by far the most numerous diaptomid in the October 1955

collections, and were second only to *D. sicilis* in the November 1954 samples. This high abundance was perhaps surprising in view of the opinions of Marsh (1893, 1895, and 1907), that *D. oregonensis* is not nearly so common as the other species in the upper Great Lakes. Eddy (1927) did not, as a matter of fact, find it at all in his southern Lake Michigan collections. It has been reported to be abundant in Georgian Bay, however, by Sars (1915). In the present study *D. oregonensis* was taken on all collection dates, but was most abundant in November; another less definite pulse occurred in July and August (table 15). A single maximum has been generally observed by other investigators (Chandler 1940 in Lake Erie, April-September; Davis 1954 in Lake Erie, July-October; Langford 1938 in Lake Nipissing, late July and August; Birge 1898 in Lake Mendota, late May and June; Marsh 1903 in Lake Winnebago, June-November).

D. oregonensis was concentrated above the metalimnion, although a few were taken below this level. Diurnal movement resembled that of the other diaptomids in that definite movement to the surface took place at night. This tendency for some reason was not so marked in 1955. Mature males of the species moved up at night on 3 of 5 dates in Lake Nipissing (Langford 1938). Juday (1903) reported a marked increase of *D. oregonensis* at the surface at night in Winona Lake, Indiana, but Birge (1895) observed no vertical movement in Lake Mendota, Wisconsin.

Copepodites of *Diaptomus*

A description of the seasonal changes of abundance of the copepodites of *Diaptomus* is difficult because mature females were combined with the copepodites in the enumerations (table 16). A fairly reliable estimate of copepodite numbers on each collection date was arrived at, however, by assuming that the mature males and females were of approximately equal numbers on any given date, and subtracting the number of mature males from the combined figures for mature females and copepodites. The above assumption may be risky, but Davis (1954) indicated that adult males and females were equally represented in his Lake Erie collections, at least in midsummer. The calculated numbers of copepodites included, of course, only those immature individuals large enough to be

taken in No. 2 bolting silk; thus all nauplii and metanauplii and probably some small copepodites were excluded.

The abundance of copepodites in 1954 was low in early June, much higher in late June, at a peak in July and early August, moderately high in late August, at another maximum in early October, and low in November. The estimation of low abundance in early June was based on the assumption that no concentrations existed below 10 meters, since no deeper samples were taken in that period. The 1955 calculations show a progressively higher number of copepodites during the three collection periods of late June, late July, and early October, but a decrease could have oc-

TABLE 16.—Total adult female and immature *Diaptomus* per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

Date and time	Surface	Depth in meters				
		5	10	20	30	40
<i>1954</i>						
June 6, 7:						
2:00 p.m.	0		2,300			
4:00 p.m.	0		1,100			
6:00 p.m.	10		1,000			
8:40 p.m.	150		940			
10:00 p.m.	590		980			
12:00 p.m.	820		790			
1:00 a.m.	460					
June 27, 28:						
10:00 p.m.			3,900			
12:00 p.m.	3,400		1,900	1,300	360	
2:00 a.m.	4,000			1,700		
4:00 a.m.	2,500		3,000	1,700	1,100	
July 16, 17:						
7:00 p.m.	310		4,000	4,800	1,600	640
2:00 p.m.	2,600		2,500	2,400	1,100	640
11:00 p.m.	4,500		2,100	3,200	1,200	540
1:00 a.m.	3,900		2,600	3,700	980	700
3:00 a.m.	3,800		1,700	3,500	1,300	520
4:30 a.m.	1,500		3,500	2,500	1,000	540
August 7:						
5:30 p.m.	70		4,900	3,800	970	990
7:45 p.m.	3,100		4,300	2,900	1,200	590
9:30 p.m.	2,500		3,200	3,300	1,300	1,000
11:00 p.m.	3,400		2,600	2,300	990	1,100
August 27:						
5:45 p.m.	40		580	4,100	2,000	
7:30 p.m.	180		870	3,500		720
9:00 p.m.	1,900		1,500	3,500	1,500	1,300
11:00 p.m.	1,400		1,900	5,600		660
October 7:						
5:15 p.m.	1,500		5,300	2,900	490	570
7:00 p.m.	6,400		7,400	1,800	550	
9:15 p.m.	4,700		5,100	1,900	810	380
November 18:						
4:30 p.m.	1,300		3,800	830	500	310
6:00 p.m.	5,900		5,500	620	840	
8:00 p.m.	4,900				540	400
10:00 p.m.	5,900		1,700	1,100	560	
<i>1955</i>						
June 30:						
6:00 p.m.	430	1,300	1,000	1,500	2,900	510
9:20 p.m.	920	1,700	1,100	940	1,100	1,300
11:30 p.m.	1,400	1,600	1,300	2,000	960	300
July 24:						
4:15 p.m.	110	2,200	7,700	7,900	1,200	120
6:15 p.m.	410	1,300	3,400	2,900	430	130
8:15 p.m.	1,200	2,900	5,400	3,700		220
10:45 p.m.	4,100	5,100	4,100	2,300	300	70
October 2:						
2:00 p.m.	160	3,200	6,300			
4:20 p.m.	450	6,400	4,800	5,000	870	5,800
6:30 p.m.	3,300	7,100	4,100	1,800	1,300	1,900
8:20 p.m.	4,100	8,400	4,200	1,200	920	460
10:30 p.m.	4,400	2,200			1,000	

curred between the latter two dates. Davis (1954) reported juvenile diaptomids most common in Lake Erie from May to October.

Because the diaptomids in the samples were largely copepodites during the summer and early fall, especially the latter, an estimate of vertical distribution and movement of the copepodites may be made by reference to the figures for combined female and immature *Diaptomus* for these months. Nothing more than general observations would be justified, however, since several species were combined and each may act differently from the others. The juveniles favored the upper layers, but not so sharply as the adults. The large numbers of copepodites at the 20-meter level in late August 1954 suggests a concentration in the metalimnion at that time. Practically all the diaptomids at the 30- and 40-meter levels during summer and early fall were copepodites, except for a fair number of *D. ashlandi*. The juveniles, like the mature males of all species, moved upward at night. Ordinarily this migration was not pronounced below 20 meters, but during the October 1955 sampling, when the *Diaptomus* population consisted almost exclusively of immature individuals, the numbers decreased successively at the 40-meter level during the afternoon and evening. Langford (1938) found copepodites of *D. oregonensis* in Lake Nipissing almost entirely below the metalimnion, where they moved very little diurnally. Juveniles of *D. minutus* at the same time were mostly above the metalimnion.

Limnocalanus macrurus

Limnocalanus macrurus was common in all series of collections in 1954 and 1955 (table 17). The numbers varied little throughout the season except for an indication of a maximum in early June. The species was present in only small numbers in the May 1958 samples, but the collections are too few for a reliable estimate of the population size at that time. Eddy (1927) found *Limnocalanus* in only the September 1888 samples of his collections from shallow water in the vicinity of Chicago, but Forbes (1882) considered the species abundant in southern Lake Michigan. Its presence has been reported by most of the other zooplankton investigators in the Great Lakes. Marsh (1898) found *Limnocalanus* throughout the year in Green Lake, Wisconsin, with peaks of

abundance in November and especially in May. In Lake Nipissing, however, Langford (1938) reported considerably fewer in May than during the summer.

In the present study *Limnocalanus* was taken primarily in the deeper layers, but it frequently migrated to the surface at night. A sharp metalimnion definitely hindered the vertical movement but did not always stop it. Figure 3 presents graphically the migration when the metalimnion was pronounced and when it was weak. A few individuals were taken at the surface when the water temperature was 20.6° C., but many more appeared there when the temperature was

TABLE 17.—*Limnocalanus macrurus* per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1954						
June 6, 7:						
2:30 p.m.	0		0			
4:00 p.m.	0		5			
6:00 p.m.	(¹)		1			
8:40 p.m.	8		89			
10:00 p.m.	2,900		340			
12:00 p.m.	1,100		190			
1:00 a.m.	850					
June 27, 28:			190			
10:00 p.m.			600	140	59	
12:00 p.m.	19			240		
2:00 a.m.	11		9	280	180	
4:00 a.m.	0					
July 16, 17:			7	4	180	83
7:00 p.m.	0		350	430	40	40
9:00 p.m.	0		0	380	42	14
11:00 p.m.	0		0	410	76	28
1:00 a.m.	0		0	360	68	37
3:00 a.m.	0		3	230	110	70
4:30 a.m.	0					
August 7:			0	180	78	95
5:30 p.m.	0		0	280	97	120
7:45 p.m.	0		0	320	90	52
9:30 p.m.	0		5	400	73	32
11:00 p.m.	2					
August 27:			0	2	150	
5:45 p.m.	0		0	140		44
7:30 p.m.	0		20	170	100	42
9:00 p.m.	0		1	330		49
11:00 p.m.	0					
October 7:			1	11	39	100
5:15 p.m.	0		6	79	85	
7:00 p.m.	3		20	10	200	82
9:15 p.m.	8					
November 18:			2	1	47	170
4:30 p.m.	2		7	41	340	
6:00 p.m.	15				130	56
8:00 p.m.	72		110	62	110	59
10:00 p.m.	28					
1955						
June 30:			0	8	31	45
6:00 p.m.	0	0	2	4	120	9
8:30 p.m.	0	2	9	12	32	18
11:30 p.m.	8	16				
July 24:			5	110	90	78
4:15 p.m.	0		19	100	69	37
6:15 p.m.	22		65	57	210	82
8:15 p.m.	58		69	150	70	63
10:45 p.m.	690					
October 2:			1			34
2:00 p.m.	0	0	1	0	0	5
4:20 p.m.	0	0	2	0	5	10
6:30 p.m.	0	0	3	5	24	18
8:20 p.m.	1	0	2	2	28	
10:30 p.m.	6	0				

¹ Calculated value less than 0.5.

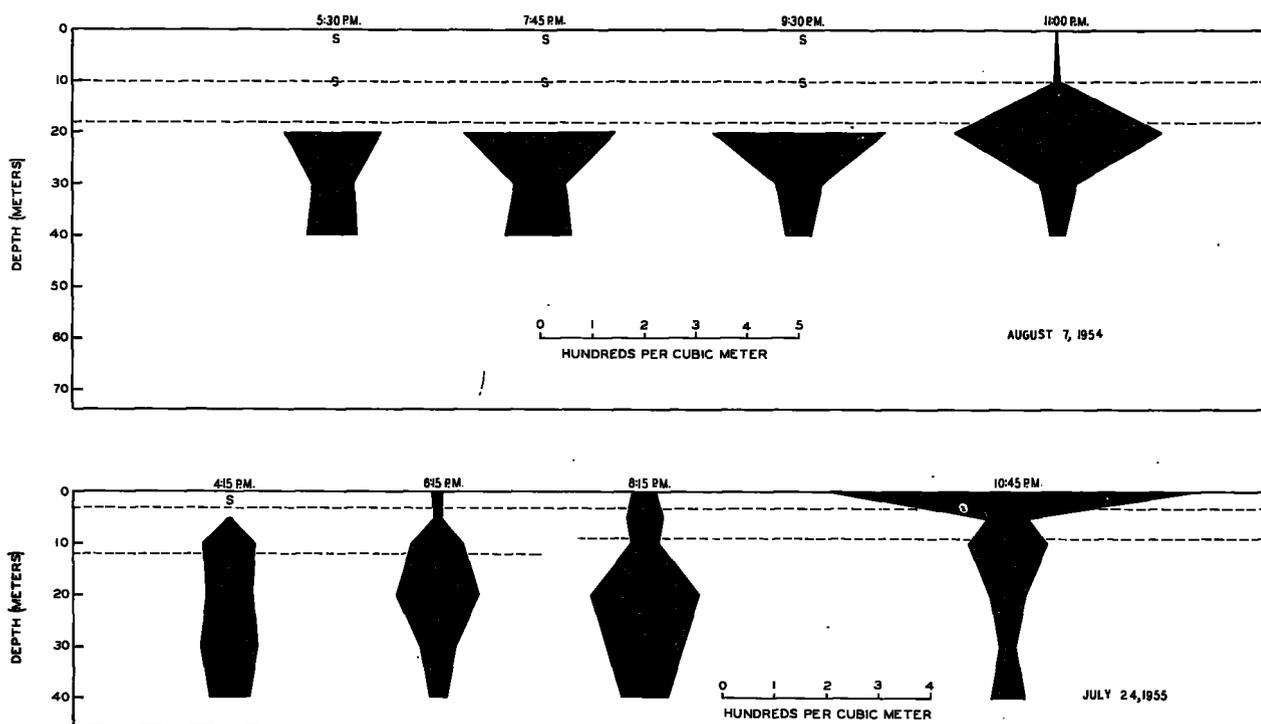


FIGURE 3.—Vertical distribution of *Limnocalanus macrurus* on August 7, 1954 (sunset 8:00 p.m.), and July 24, 1955 (sunset 8:15 p.m.; Eastern standard time). The broken lines represent the limits of the metalimnion. The metalimnion was pronounced on August 7. On July 24 it was distinct at 4:15, less so at 6:15, and weak at 8:15 and 10:45 (see fig. 1). The bottom line of each panel shows the depth of the lake at the sampling locality. No samples were taken below 40 meters; an S indicates samples in which *L. macrurus* did not occur.

8–10° lower. Maximum numbers reached the surface one and one-half to four hours after sunset, but a few were present there two hours before sunset in July 1955, probably as a result of the upwelling on that date. The June 1954 data suggest that the species begins to leave the surface soon after its peak is reached and probably deserts this level by sunrise or sooner. Observations of other investigators suggest, however, that *Limnocalanus* may not always avoid the surface in bright daylight. It has been found in surface samples which presumably were collected in full daylight from comparatively shallow water in Lakes Michigan, Superior, and Erie (Eddy 1927 and 1943, Wilson 1929). In Lakes Superior and Erie the species was actually most abundant at the surface. In the deeper areas of Lake Erie, however, it was almost wholly confined to the lower strata. The same situation prevailed in the deep water of Lake Nipissing (Langford 1938). Juday (1904) reported that in Green Lake, Wis-

consin, *Limnocalanus* was not found in the epilimnion, but migrated up to the metalimnion at night.

Epischura lacustris

Although it was never extremely numerous, *Epischura lacustris* was taken on every collection date except May 1958 (table 18). It was less common in early June and November than in the summer of 1954. All individuals in the early June collections were very small juveniles. Thus the evidence is strong that this species is absent in Lake Michigan during the winter and early spring. The density of the summer population varied little. The small number in July 1955 was probably a result of the upwelling. Forbes (1882) was the first to report *Epischura* from Lake Michigan (Grand Traverse Bay). Marsh (1895) found it common in the Traverse Bay region. Eddy (1927) did not find it in southern Lake Michigan in one year, but it was abundant from April to November (lacking at other times) in

another. The species has been reported as common in Lake Superior (Forbes 1891) and very abundant in Georgian Bay (Sars 1915). In Lake Erie, Davis (1954) found the form most common in May–October, and Chandler (1940) reported it present in April–October. Apparently disappearance in winter is normal in small lakes also (Marsh 1898 and 1903).

Relatively few *Epischura* were found below the metalimnion in the present study. The species was most plentiful at 10 meters and above in late June, July, and August, when the top of the metalimnion was at 10 meters, but its relative numbers were high at 20 meters in October and

TABLE 18.—*Epischura lacustris* per cubic meter of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

Date and time	Surface	Depth in meters				
		5	10	20	30	40
<i>1954</i>						
June 6, 7:						
2:00 p.m.	0		0			
4:00 p.m.	(¹)		0			
6:00 p.m.	21		0			
8:40 p.m.	10		0			
10:00 p.m.	5		0			
12:00 p.m.	1		0			
1:00 a.m.	0					
June 27, 28:						
10:00 p.m.			2			
12:00 p.m.	93		1	1	1	
2:00 a.m.	48			0		
4:00 a.m.	54		15	0	0	
July 16, 17:						
7:00 p.m.	11		4	3	2	0
9:00 p.m.	78		82	3	3	3
11:00 p.m.	260		93	2	6	3
1:00 a.m.	1,400		30	2	3	6
3:00 a.m.	85		42	1	4	(¹)
4:30 a.m.	98		11	0	1	1
August 7:						
5:30 p.m.	0		6	4	1	1
7:45 p.m.	25		57	1	3	3
9:30 p.m.	490		56	1	2	1
11:00 p.m.	130		33	0	1	6
August 27:						
5:45 p.m.	0		58	3	0	0
7:30 p.m.	0		47	2		0
9:00 p.m.	420		18	0	2	1
11:00 p.m.	260		19	4		1
October 7:						
5:15 p.m.	0		47	13	5	2
7:00 p.m.	77		25	23	3	
9:15 p.m.	6		17	46	6	2
November 18:						
4:30 p.m.	21		2	1	0	(¹)
6:00 p.m.	140		2	3	1	
8:00 p.m.	1				1	0
10:00 p.m.	0		0	8	0	0
<i>1955</i>						
June 30:						
6:00 p.m.	1	6	22	0	3	1
8:30 p.m.	17	9	8	0	0	2
11:30 p.m.	12	74	6	1	0	0
July 24:						
4:15 p.m.	0	10	0	0	0	0
6:15 p.m.	1	1	1	1	0	0
8:15 p.m.	.9	1	0	0		0
10:45 p.m.	1	0	0	0	0	0
October 2:						
2:00 p.m.	0	92	150			
4:20 p.m.	2	15	150	46	8	17
6:30 p.m.	6	10	120	71	28	0
8:20 p.m.	130	59	24	68	24	0
10:30 p.m.	47	12	31	44	22	1

¹ Calculated value less than one.

November when the metalimnion was below this level. Without exception *Epischura* moved toward the surface at night. The main movement was in the epilimnion, but some individuals appeared to move up from the metalimnion, since the numbers just above this level occasionally increased at the same time the numbers were increasing at the surface. Large concentrations must have existed at depths not sampled, probably between the surface and 10 meters, because the numbers in the surface samples often increased far out of proportion to the decreases in the samples from lower levels. Although some *Epischura* usually were at the surface by sunset, or even somewhat before, the maximum numbers ordinarily did not appear until one to one and one-half hours after sunset. Numbers at the surface then decreased except possibly for a small increase near dawn.

The July 16–17 observations offer a notable exception to the usual migration. At this time the maximum abundance at the surface was not reached until 1:00 a.m., when unusually large numbers were taken. This apparently aberrant behavior has no obvious explanation, but it might have been caused by the brightness of the moonlight throughout the night. The moon was full also on June 30 and October 2, but few *Epischura* were present June 30 and the moon did not become bright until nearly midnight on October 2.

Vertical distribution and movements of *Epischura lacustris* in Lake Michigan are similar to those in several other lakes. Marsh (1898) and Maloney and Tressler (1942) found this species to be most abundant in the upper, warm regions of Green Lake, Wisconsin, and Caroga Lake, New York, respectively. They came to the surface within 1/2 to 1 1/2 hours after sunset in Winona Lake, Indiana (Juday 1903), and within 1 hour after sunset in several Wisconsin lakes (Juday 1904).

Senecella calanoides

Although it was uncommon at all times, *Senecella calanoides* was taken in every collection period except early June 1954 and May 1958 (table 19). This species has not been previously found in Lake Michigan. Marsh (1933), however, reported immature forms from Pine Lake (Lake Charlevoix), Michigan, which is connected to Lake Michigan by a short channel. Immature

individuals were also found in Lake Superior by Marsh (1933). The species was found in a single cisco stomach from Lake Ontario (Pritchard 1931). There are no other reports of occurrences in the Great Lakes, but *Senecella* is known to occur in several other deep lakes in North America (Juday 1923; Rawson 1956). Nothing has been published previously of its seasonal abundance, nor can estimates of seasonal population changes be made here, since the numbers of individuals taken are much too small.

Senecella is regarded as a deep- and cold-water form, a view borne out by the present study. The evidence suggests that most individuals spend the bright daylight hours very near the bottom, but begin ascending before dark. On two occasions in 1955, when the deepest (40-meter) samples were collected only 6 meters above the bottom, no

TABLE 19.—*Senecella calanoides* per 10 cubic meters of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

[None taken June 6-7, 1954]

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1954						
June 27, 28:						
10:00 p.m.	0		11			
12:00 p.m.	0		0		40	
2:00 a.m.	0			10		
4:00 a.m.	0		0	0	0	
July 16, 17:						
7:00 p.m.	0		0	15	0	0
9:00 p.m.	0		0	0	0	0
11:00 p.m.	0		0	0	0	4
1:00 a.m.	0		0	0	17	11
3:00 a.m.	0		0	0	7	10
4:30 a.m.	0		0	0	3	14
August 7:						
5:30 p.m.	0		0	0	4	0
7:45 p.m.	0		0	0	0	5
9:30 p.m.	0		0	0	13	5
11:00 p.m.	0		0	8	7	0
August 27:						
5:45 p.m.	0		0	0	0	6
7:30 p.m.	0		0	0	0	12
9:00 p.m.	0		5	0	13	12
11:00 p.m.	0		0	0	0	12
October 7:						
5:15 p.m.	0		0	0	0	0
7:00 p.m.	0		0	5	9	0
9:15 p.m.	0		0	16	44	14
November 18:						
4:30 p.m.	0		0	0	4	3
6:00 p.m.	0		0	6	57	35
8:00 p.m.	0		0	0	60	35
10:00 p.m.	22		0	12	112	18
1955						
June 30:						
6:00 p.m.	0	0	0	0	0	0
8:30 p.m.	0	0	0	0	0	18
11:30 p.m.	0	0	0	0	0	8
July 24:						
4:15 p.m.	0	0	0	0	0	0
6:15 p.m.	0	0	14	0	0	44
8:15 p.m.	0	0	0	14	0	52
10:45 p.m.	0	39	11	30	10	43
October 2:						
2:00 p.m.	0	0	0	0	0	14
4:20 p.m.	0	0	0	0	0	0
6:30 p.m.	0	24	0	0	0	0
8:20 p.m.	0	0	0	0	13	0
10:30 p.m.	0	0	0	0	11	0

Senecella were found in any of the samples of the first afternoon series, but they were present in all the subsequent series. The species often appeared in samples taken from levels well above the bottom somewhat before dusk. It usually avoided the warm upper layers, and was found at the surface only once (Nov. 1954), when the surface-water temperature was 10.9° C.

The literature contains no mention of the vertical migration of *Senecella*.

AMPHIPODA

Pontoporeia affinis

Pontoporeia affinis was taken in small numbers during every collecting period except October 1955 and May 1958 (table 20). It is generally regarded as a bottom form, although Pennak (1953) stated that it also may be in the plankton. It showed a definite affinity for the deeper, cold water but came to the surface during early June and November when the surface-water temperatures were 10.3° and 10.9° C., respectively. It usually avoided temperatures warmer than these, and was rarely above the metalimnion. In October 1954, however, it was taken from 10 meters where the temperature was 16.7° C.

The vertical migration of *Pontoporeia* was rapid. Because the species never appeared in samples taken before sunset, it is assumed to have been on the bottom during the daytime. In November 1954, none were present in a series of samples collected between 4:30 and 5:30 p.m. (sunset 5:15 p.m.), but the presence of several in the surface sample at 6:00 p.m. suggests that some individuals moved at least 40 and possibly 74 meters (from the bottom) vertically in one-half hour or less.

No large-scale vertical migration of *Pontoporeia* has been reported before, at least in North America. In Great Slave Lake, however, it was observed to come to the surface in shallow water (1 or 2 meters deep) just before dark (Larkin 1948). It reached a peak about 1 hour later and then decreased until dawn. The data from the November samples provide evidence that in Lake Michigan *Pontoporeia* shows a similar migration pattern, but the numbers are too small for definite conclusions. Neither can anything be concluded regarding the percentage of the total population which migrates. It is known that some remain

TABLE 20.—*Pontoporeia affinis* per 10 cubic meters of water off Grand Haven, Mich., in 1954 and off Frankfort, Mich., in 1955

[None taken October 2, 1955]

Date and time	Surface	Depth in meters				
		5	10	20	30	40
1954						
June 6, 7:						
2:00 p.m.	0	0	0	0	0	0
4:00 p.m.	0	0	0	0	0	0
6:00 p.m.	0	0	0	0	0	0
8:40 p.m.	2	0	0	0	0	0
10:00 p.m.	11	0	0	0	0	0
12:00 p.m.	5	2	0	0	0	0
1:00 a.m.	8	0	0	0	0	0
June 27, 28:						
10:00 p.m.	0	3	0	0	0	0
12:00 p.m.	0	0	2	4	0	0
2:00 a.m.	0	0	0	0	0	0
4:00 a.m.	0	0	0	0	0	0
July 16, 17:						
7:00 p.m.	0	0	0	0	0	0
9:00 p.m.	0	0	0	0	0	1
11:00 p.m.	0	0	0	0	2	2
1:00 a.m.	0	0	0	0	0	1
3:00 a.m.	0	0	1	0	1	0
4:30 a.m.	0	0	0	0	1	0
August 7:						
5:30 p.m.	0	0	0	0	0	0
7:45 p.m.	0	0	0	1	0	0
9:30 p.m.	0	0	2	1	0	0
11:00 p.m.	0	0	0	1	2	0
August 27:						
5:45 p.m.	0	0	0	0	0	0
7:30 p.m.	0	0	0	0	0	0
9:00 p.m.	0	0	0	0	0	0
11:00 p.m.	0	0	0	0	0	1
October 7:						
5:15 p.m.	0	0	0	0	0	0
7:00 p.m.	0	1	0	0	0	0
9:15 p.m.	0	0	0	0	0	1
November 18:						
4:30 p.m.	0	0	0	0	0	0
6:00 p.m.	23	0	0	3	0	0
8:00 p.m.	11	1	0	1	1	0
10:00 p.m.	5	0	0	1	0	0
1955						
June 30:						
6:00 p.m.	0	0	0	0	0	0
8:30 p.m.	0	0	0	0	0	7
11:30 p.m.	0	5	0	4	0	16
July 24:						
4:15 p.m.	0	0	0	0	0	0
6:15 p.m.	0	0	0	3	0	0
8:15 p.m.	0	0	0	0	0	0
10:45 p.m.	0	1	1	2	0	3

on the bottom, because they have been abundant in dredge samples taken from the bottom at night.

Juday (1904) found the amphipod *Gammarus* in surface samples at night in limnetic regions of Wisconsin lakes where the water was 18 meters or more deep. Since he never found it in the surface samples taken during the day, he concluded that it migrated horizontally from the littoral region at night.

MYSIDACEA

Mysis relicta

Data from the present samples on the vertical migration of *Mysis relicta* were part of a detailed study by Beeton.² Only a brief summary of

² Beeton, Alfred M. The vertical migration of *Mysis relicta* in Lakes Huron and Michigan. Doctoral dissertation, University of Michigan, ix + 131 pp. 1957.

Beeton's findings is presented here since details are to be included in a publication by that investigator.

Mysids were concentrated within 1 or 2 meters of the bottom during the day but migrated into the upper strata at night. Light is the most important factor in the initiation and control of their vertical movement. They usually ascended when the surface light intensity was decreasing from 15 to 1 foot candle, and descended when the surface light intensity was increasing from 10^{-3} to 10^{-2} foot candle. Thermal conditions also affected vertical distribution. The degree of temperature change was more effective in limiting vertical distribution than actual temperature. In early evening the mysids frequently migrated through the metalimnion, but later at night the distribution changed and a maximum concentration of mysids occurred in or immediately beneath the metalimnion. This downward movement was more pronounced among the sexually differentiated mysids than with the younger ones; the latter were more inclined to remain above the metalimnion. The vertical migration of male and female mysids was closely similar.

No striking differences in seasonal abundance of *Mysis relicta* were apparent, but numbers are too small for definite conclusions.

SUMMARY

(1) Day-and-night zooplankton collections were made in Lake Michigan on seven occasions between June 6 and November 18, 1954, and on 3 occasions between June 30 and October 2, 1955. The 1954 sampling area was about 8 miles off Grand Haven, Michigan, at a depth of 74 meters and the 1955 sampling area was about 3 miles offshore near Frankfort, Michigan, at a depth of 46 meters. Limited sampling was also done off Sturgeon Bay, Wisconsin, on May 4, 1958.

(2) Collections were made with a Clarke-Bumpus plankton sampler with a net of No. 2 bolting silk. Series of samples were taken at about 2-hour intervals; each series usually included 10-minute tows from the surface and at depths of 10, 20, 30, and 40 meters in 1954 and 5-minute tows from the surface and at 5, 10, 20, 30 and 40 meters in 1955.

(3) Subsamples were employed for the enumeration of most species, but total counts were made

of *Polyphemus*, *Leptodora* (usually), *Pontoporeia*, and *Mysis*.

(4) Twenty-four species of crustaceans were observed in the samples; 4 of them (*Polyphemus pediculus*, *Eurycerus lamellatus*, *Cyclops vernalis*, and *Senecella calanoides*) are reported from Lake Michigan for the first time. Data permitted an analysis of seasonal distribution for 15 species and of vertical migration for 19 species.

(5) Most species of crustaceans in Lake Michigan reach only one population peak a year, and many apparently are present only as eggs in winter and early spring.

(6) All species taken in sufficient numbers for study showed some degree of vertical migration. Diurnal changes in light intensity had a major influence on the migration. Most species migrated to the surface late in the day, and had peaks at that level near sunset or soon afterwards. Numbers at the surface commonly decreased toward midnight, and for some species, according to the limited evidence, increased between midnight and dawn. Water temperatures also affected vertical movements, especially of cold-water forms. A few species were reluctant to migrate up through a pronounced metalimnion.

(7) *Daphnia galeata mendotae*.—Population peak early August in 1954, but greatest numbers in 1955 in October samples; probably absent in winter and early spring; strongly partial to the upper layers; vertical movement below metalimnion limited, but evidence of considerable movement up from the metalimnion; young usually taken at surface earlier than adults.

(8) *Daphnia retrocurva*.—Population changes much like *D. galeata*, except probably absent for greater length of time in winter and spring; vertical distribution and migration similar to *D. galeata*.

(9) *Bosmina longirostris*.—(Limited data). Indefinite suggestion of early summer population peak; probably absent in winter; preference for upper layers; migration toward surface late in day, downward during the middle of the night and again toward surface at dawn.

(10) *Diaphanosoma brachyurum*.—(Limited data). Abundance at maxima in early summer and fall of 1954 and fall of 1955; probably absent in winter and early spring; preference for upper levels; definite increase at surface early in night.

(11) *Holopedium gibberum*.—Taken only in July and October, 1955; probably absent in winter and spring; not found below metalimnion; increased at surface near sunset.

(12) *Sida crystallina*.—Taken only in October 1955; none below metalimnion; some at surface at night.

(13) *Leptodora kindti*.—Most abundant in July and early August 1954 and in October 1955; most common in upper strata; maximum numbers at surface early in night.

(14) *Polyphemus pediculus*.—Taken only in summer; preference for upper levels; some at surface in afternoon, but more early in night.

(15) *Cyclops bicuspidatus*.—Probably present year-round; population pulse late spring and early summer, possibly again in late fall; most plentiful in upper layers but on occasion in moderately large numbers below metalimnion; strong migration to surface at night; indication of some movement through metalimnion.

(16) *Mesocyclops edax*.—No striking population changes from late June to early October, but species scarce or absent at other times; more nearly restricted to epilimnion than *Cyclops bicuspidatus*; pronounced increase in numbers at surface at night; probably no movement through metalimnion.

(17) *Diaptomus minutus* (adult males).—Most abundant in late June and scarcest in October; strong preference for upper levels; migration to surface at night pronounced.

(18) *Diaptomus sicilis* (adult males).—Most abundant in November and lacking in late August; preference for upper layers but plentiful at surface only after sunset.

(19) *Diaptomus ashlandi* (adult males).—Population maxima in early summer and middle or late fall; scarce in early October; preference for upper strata less strong than in other adult male diaptomids; migration to surface at night definite.

(20) *Diaptomus oregonensis* (adult males).—Most abundant in mid-November; less definite pulse in July and August; primarily in epilimnion; strong migration to surface at night.

(21) Copepodites of *Diaptomus*.—Population peaks from mid-July to early August and in early October; preference for upper levels less strong than in adult males; migration similar to adults.

(22) *Limnocalanus macrurus*.—Fairly uniform in number throughout season, possible population peak in early June; distributed primarily in deeper layers, but occasionally at surface at night; vertical movement hindered but not always blocked by a sharp metalimnion.

(23) *Epischura lacustris*.—Most common in summer; probably absent during winter and early spring; scarce below metalimnion; main vertical migration apparently in epilimnion, but some movement up from the metalimnion probable.

(24) *Senecella calanoides*.—Present during all collection periods except early June 1954 and May 1958; collections too small to estimate seasonal abundance; most individuals apparently

near bottom by day; ordinarily no migration through metalimnion; found at the surface in November 1954 when thermal stratification was weak (surface-water temperatures 10.9° C.).

(25) *Pontoporeia affinis*.—No basis for estimate of seasonal abundance; on or near bottom during daytime; rapid vertical migration at night; at surface during only early June and mid-November (water temperatures 10.3° and 10.9° C., respectively).

(26) *Mysis relicta*.—No basis for estimate of seasonal abundance; concentrated within 1 or 2 meters of bottom during the day; occasional migration through metalimnion at night; stay of adults in epilimnion usually short.

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**SYSTEMATICS AND BIOLOGY OF THE
GIZZARD SHAD (*DOROSOMA CEPEDIANUM*)
AND RELATED FISHES**

BY ROBERT RUSH MILLER



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ABSTRACT

The gizzard shads, marine and fresh-water herrings of the subfamily Dorosomatinae, are characterized and keys are given to the seven known genera and to the five species of the American genus *Dorosoma* (*Signalosa* is regarded as a subgenus). The systematics and biology of the eastern gizzard shad, *Dorosoma cepedianum*, are treated in detail. The biological information results largely from a critical survey of papers (unpublished as well as published) dealing with its fecundity, reproduction and development, size, age and growth, abundance, habitat and migration, mortality, parasites and predators, and its food, forage value, and utilization by man. Original drawings of early life-history stages are presented. This summary should enable fishery biologists concerned with inland waters to gain a more comprehensive outlook on the role of the gizzard shad in fish management.

SYSTEMATICS AND BIOLOGY OF THE GIZZARD SHAD (*DOROSOMA CEPEDIANUM*) AND RELATED FISHES

By ROBERT RUSH MILLER, *Curator of Fishes,*
Museum of Zoology, University of Michigan

The herrings of the subfamily Dorosomatinae, known as gizzard and threadfin shads in the New World, comprise seven genera inhabiting Asia, the Indo-Australian region, and North America. Fishery biologists dealing with management of inland waters in eastern North America have been increasingly concerned about the role of the gizzard shad, *Dorosoma cepedianum*, in the ecology of fish populations. Praised in some places as a valuable forage fish, this widespread species has elsewhere so overpopulated lakes that costly and time-consuming control measures have become necessary. A review of the systematics and biology of this species should make possible a more critical assessment of its part in fish management. The present paper is designed to summarize what is known of gizzard shads in general and of *D. cepedianum* in particular.

As a group, the gizzard shads are characterized by the inferior, subterminal or terminal, toothless mouth and the gizzardlike stomach; they were first recognized under the name *Chatoëssina* by Günther (1868: 381, 406). The unit was raised to family rank, Dorosomidae, more properly Dorosomatidae, by Gill (1872: 17), and was retained at this level for many years, at least by American ichthyologists. Most workers now refer the group to the Clupeidae and relegate the gizzard shads at most to a subfamily, Dorosomatinae, as did Berg (1940).

The body is generally short and deep (except in the slender young) and moderately to strongly compressed. The scales are thin, cycloid, and more or less adherent; they are absent on the head and may be present or absent on the back between the occiput and the dorsal fin. The abdomen is compressed to a ridge and armed with keeled, bony scutes. The eyes have conspicuous adipose "eyelids." The gill membranes are sepa-

rate and free from the isthmus; the gill rakers are slender, close set, and exceedingly numerous. There are five to six branchiostegals, and the pseudo-branchiae are large.

Regan (1917: 297) included this subfamily in the Clupeinae because he regarded the separation of the gizzard shads from the other genera centering about *Clupea* as an artificial arrangement. I have not studied the Old World genera and can neither confirm nor dispute Regan's viewpoint. However, since there has been no comprehensive study of the species and genera now referred to the Dorosomatinae, the interrelationships of the Old and New World forms should be regarded as tentative.

As a whole, the gizzard shads are migratory fishes, primarily marine, entering fresh or brackish waters to spawn. Some species, and some populations of single species (such as *Dorosoma cepedianum* and *D. petenense*), are landlocked, completing their life cycle wholly in fresh water. Their food, except early in life, consists chiefly of minute organic particles which are strained by the fine, abundant gill rakers, aided by the accessory pharyngeal pockets (Lagler and Kraatz, 1945; Iwai 1956). The stomach is a short, thick-walled muscular structure like the gizzard of a fowl; the intestine is long and much convoluted, with numerous folds on its inner surface and hundreds of pyloric caeca externally. These digestive specializations further serve to assimilate the minute food of these fishes.

All but two of the seven genera, *Anodontotoma* and *Goniulosa*, are further characterized by having the last dorsal ray prolonged into a conspicuous, elongated filament in the adult. Only *Dorosoma* (including *Signalosa*) inhabits the New World; the other genera are found in Asia and the Indo-Australian region.

In surveying the literature dealing with the

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biology of *Dorosoma cepedianum*, I have been assisted very materially by the index and references in the library of John van Oosten. Others who have aided in supplying data or references are Reeve M. Bailey, George W. Bennett, S. M. Bower, Gerald P. Cooper, Robert Cummins, Jr., Alfred W. Eipper, Ralph Hile, Melvin T. Huish, Alfred Larsen, Foster D. Roszman, Milton B. Trautman, C. R. Robins, and E. L. Wickliff. I am particularly indebted to Edward N. Warner

for allowing me to publish his original drawings (figs. 2-4) and to summarize unpublished material from his doctoral thesis, and likewise to Anthony Bodola for permission to use data from his doctoral dissertation. William L. Brudon made the drawing of the adult (fig. 1).

In the following key, the separation of the Asiatic genera is based on the data given by Regan (1917: 298, 308-317) and on the synopsis presented by Herre and Myers (1931: 234-236).

KEY TO GENERA OF DOROSOMATINAE

- 1a. Maxillary provided with two supramaxillary bones (the anterior one thinner and more scalelike than the posterior one).....New World (*Dorosoma*)
- 1b. A single supramaxillary bone.....(Old World genera) 2
- 2a. Last ray of dorsal fin produced into a conspicuous filament..... 3
- 2b. Last ray of dorsal fin not produced into a filament or only weakly so.....(*Anodontostoma* and *Gonialosa*) 5
- 3a. Maxillary flattened, wide posteriorly, without a downward curve at its distal tip; gill rakers of posterior end of ceratohyal nearly as long as longest opposite gill filaments..... 4
- 3b. Maxillary little flattened, very narrow, with a downward angle at its distal tip; gill rakers of posterior part of ceratohyal only half or less than half as long as the opposite gill filaments...*Nematalosa* Regan
- 4a. Dentary normal, not reflected outward, fitting well up inside upper jaw with mouth closed.....*Clupanodon* Lacépède.
- 4b. Dentary anterior to point where it appears from beneath upper jaw (with mouth closed) with its sharp ramus reflected outward, its edge opposed to edge of upper jaw.....*Konosirus* Jordan and Snyder
- 5a. Maxillary straight, thin, transversely expanded, tapering distally. Last dorsal ray little if at all produced.....*Anodontostoma* Bleeker
- 5b. Maxillary slender, distally slightly expanded and curved downwards. Last dorsal ray not produced.....*Gonialosa* Regan

Genus *Dorosoma* Rafinesque

Gizzard shads, threadfin shad

Dorosoma Rafinesque, Western Rev. and Misc. Mag., 1820: 2 (3): 171 (see Fowler 1945: 6, 8); Ichthyologia Ohniensis, 1820: 39. Type species by monotypy, *D. notata* = *D. cepedianum* (LeSueur). Type locality: Below the falls of the Ohio River.

Signalosa Evermann and Kendall, 1898, Bull. U.S. Fish Commission, 17 (1897): 127. Type species, *Signalosa atchafalaya* = *D. petenense* (Günther). Type locality: Atchafalaya River, Melville, La.

Common name.—The fishes of this genus have generally been referred to as gizzard shads because of the gizzardlike muscular stomach. The vernaculars, skipjack, hickory shad, mud shad, sawbelly, jack shad, et cetera, were formerly applied to *D. cepedianum* and are still used locally; the name *aucun* is used in Quebec. Threadfin shad has been adopted as the vernacular for *D. petenense*.

Generic characters.—Clupeid fishes with the last ray of the dorsal fin prolonged into a slender fila-

ment (absent or inconspicuous in the young), thus resembling their marine New World relative *Opisthonema*. The mouth is small to moderate, terminal, subterminal, or inferior, the lower jaw included or the jaws subequal. Mouth toothless in adult, but young with a row of fine teeth on upper jaw. Maxillary with two supramaxillary bones. Snout short and rounded. Stomach gizzardlike, the intestine long and much convoluted, with numerous pyloric caeca. Body compressed, silvery, the abdomen armed with bony scutes (total, 23-32). Dorsal rays 9-15; anal rays 17-38; pectoral rays 12-17, pelvic rays 8; caudal rays 19 (17 branched), rarely 17 or 18. Scales cycloid, thin, 40-83 along side. Vertebrae (including urostyle) 40-51.

Range.—All the species except *D. smithi* are confined to the Atlantic drainage of North and

Middle America (Canada to Nicaragua). They are found from the Great Lakes—St. Lawrence River basins, southern South Dakota, Nebraska, and Minnesota, and from about latitude 40° N. on the Atlantic seaboard of New Jersey and southeastern Pennsylvania southward to Lake Nicaragua (but with discontinuous distribution from northern Guatemala and British Honduras to Nicaragua). *D. smithi* is known only from coastal streams of northwestern México, in Sonora, Sinaloa, and Nayarit.¹

Species.—Five species of *Dorosoma* are recognized, four in the subgenus *Dorosoma* and one,

D. petenense, in the subgenus *Signalosa*. They may be distinguished by means of the following key. The resemblances between *Dorosoma* and *Signalosa* are numerous, the differences few, with no sharp structural gaps. The form and position of the mouth afford the most reliable means of distinction. The relationships of the five species seem to be better expressed by referring them all to *Dorosoma*, using subgenera to indicate the lesser phyletic lines.

¹The record for Nayarit is based on 123 specimens in the University of Michigan Museum of Zoology (UMMZ 171979) collected in 1955.

KEY TO SPECIES OF DOROSOMA

- 1a. Mouth terminal, ventral edge of upper jaw smooth. Fewer than 50 scales in lateral series, regularly arranged. Anal rays 17–27, usually 20–25. Vertebrae 40–45. Atlantic slope from Florida, Tennessee, and Oklahoma west and south to northern Guatemala and British Honduras.....Subgenus *Signalosa*, *D. petenense* (Günther)
- 1b. Mouth subterminal or inferior, ventral edge of upper jaw with slight to pronounced notch (except in young). More than 50 scales in lateral series, irregularly arranged. Anal rays 22–38, usually 29–35 (where range overlaps that of *Signalosa*). Vertebrae 43–51 (47–51 where the two subgenera coexist).....Subgenus *Dorosoma*
- 2a. Lateral scales 52–70, usually 58–65; scales around body 36–45; vertebrae 48–51. Atlantic drainage of eastern North America south to Río Pánuco, México.....*D. cepedianum* (LeSueur)
- 2b. Lateral scales 70–83, usually 73–78; scales around body 46–60; vertebrae 43–48..... 3
- 3a. Dorsal filament long, its length as measured from dorsal origin 0.95 to 1.4 times, usually 1.1 to 1.3, in distance from pelvic insertion to tip of snout; anal base 1.1–1.4 in same distance; anal rays 29–38, usually 32–35. Atlantic slope of México and northern Guatemala (Río Papaloapan to Río Usumacinta).....*D. anale* Meek
- 3b. Dorsal filament short, its length as measured from dorsal origin 1.4–1.85, usually 1.5–1.8, in distance from pelvic insertion to tip of snout; anal base 1.6–2.2 in same distance; anal rays 22–31, usually 23–29..... 4
- 4a. Mandible long, nearly one-half length of head; scales around caudal peduncle 20–26; dorsal rays usually 13 (12–14). Lakes Managua and Nicaragua, Nicaragua.....*D. chavesi* Meek
- 4b. Mandible short, less than one-third length of head; scales around caudal peduncle 28–31; dorsal rays usually 11–12 (9–13, rarely 9, 10, or 13). Pacific slope of northwestern México (Sonora to Nayarit).....*D. smithi* Hubbs and Miller

In this work, only *Dorosoma cepedianum* is treated in detail. Information on the systematic characters, growth, and relationships of the other three species of the subgenus *Dorosoma* appeared elsewhere (Miller 1950). Recent interest in the threadfin shad, *Dorosoma (Signalosa) petenense*, as a forage fish has resulted in the experimental planting of this species in various States (Parsons and Kimsey, 1954; Kimsey 1954). Relatively little published data is available on the systematics and biology of the threadfin shad.

Dorosoma cepedianum (LeSueur)

Eastern gizzard shad, hickory shad, skipjack, mud shad

(Figures 1–4)

Synonymy.—In the following partial synonymy, only the references to original descrip-

tions of the forms now regarded to be conspecific with *Dorosoma cepedianum* are given.

Megalops cepedianus LeSueur, 1818, Jour. Acad. Nat. Sci. Phila., 1: 361–363 (original description; markets of Baltimore and Philadelphia, hence usually given as Chesapeake and Delaware Bays).

Clupea heterura Rafinesque, 1818, Amer. Month. Mag., 1818: 354 (original description; Ohio River).

Dorosoma notata Rafinesque, 1820, Western Rev. and Misc. Mag., 2: 172 (original description; falls of the Ohio River).

Chatoëssus ellipticus Kirtland, 1838, Rept. Zool. Ohio, in Second Ann. Rept. Geol. Surv. Ohio, Columbus, 1838: 169, 195 (*nomen nudum*, Ohio; same as *Dorosoma notata*). 1844, Boston Jour. Nat. Hist., 4 (2): 235–237, pl. 10, fig. 1 (original description, comparisons, occurrence in Ohio, habits, mortality; Ohio River and its tributaries).

Chatoëssus insociabilis Abbott, 1861, Proc. Acad. Nat. Sci. Phila., 12 (1860): 365–366 (original description, habits; "sturgeon pond" 2 miles below Trenton, N.J.).

Megalops bimaculata LeSueur, 1848, in Cuvier and Valenciennes, Hist. Nat. Poiss., 21: 104 (*nomen nudum*; synonymized with *Chatoessus cepedianus* by Valenciennes).

Dorosoma cepedianum exile Jordan and Gilbert, 1883, Proc. U.S. Natl. Mus., 5 (1882): 585 (original description, based on 2 specimens, from Galveston, Tex.).

Diagnosis.—A gizzard shad with 52–70 lateral scales,² 36–45 scales around the body, 48–51 (usually 50) vertebrae, 25–36 anal rays, and preponderantly 18 + 12 ventral scutes.

The dorsal filament is comparatively long. As in the other species of *Dorosoma*, its length varies greatly with age, and statements regarding this structure have little meaning unless accompanied by data on the size of the specimen. The filament is inconspicuous or absent in young fish, increasing in length with age up to a certain size range (around 200 mm.?), and then decreasing in relative size.

Description.—Body depth 2.3–3.1 in standard length (all measurements “stepped off” with a pair of precision dividers); predorsal length 1.85–2.05; prepelvic length 2.0–2.35; anal origin to caudal base 2.4–2.8; head length 3.0–3.9; length of dorsal filament 3.1–6.5 (0.8–2.0 in head

length); length of anal base 3.2–3.9 (0.75–1.25 in head length). Head width 1.8–2.5 in head length; eye length 3.3–5.4; snout length 5.0–6.0; bony width of interorbital 3.3–4.5; length of upper jaw 3.5–4.2; length of mandible 2.6–3.3; length of caudal peduncle 2.4–3.5; depth of caudal peduncle 2.45–3.4; length of pectoral 1.15–1.45; length of pelvic 2.0–2.5; length of dorsal base 1.85–2.6; length of lower lobe of caudal 0.7–1.1, typically longer than anal base (rarely subequal).

Dorsal rays 10–13, average 11.61 in 197 specimens; anal rays 25–36, 31.32, in 195; pectoral rays 14–17, 15.52, in 288 (144 individuals); pelvic rays 8, rarely 7; and caudal rays 19. Lateral scales (first scale counted was first one lying above uppermost corner of gill opening) 52–70, 61.06, in 67; scales between dorsal and anal fins 19–24, 21.77, in 52; scales around body (beginning with first scale just in front of left pelvic fin) 36–45, 41.03, in 73; and scales around caudal peduncle (slenderest part) 16–20, 18.02, in 53. Prepelvic scutes 17–20, 17.99, in 196; postpelvic scutes 10–14, 11.76, in 197; total ventral scutes 27–32, 29.74, in 196. Number of vertebrae (including urostyle) 48–51, 49.83, in 42 specimens. Gill rakers very numerous and fine, those on first arch number about 90 to 300 at standard lengths of

² For method of counting scales see Miller (1950: 388–389).

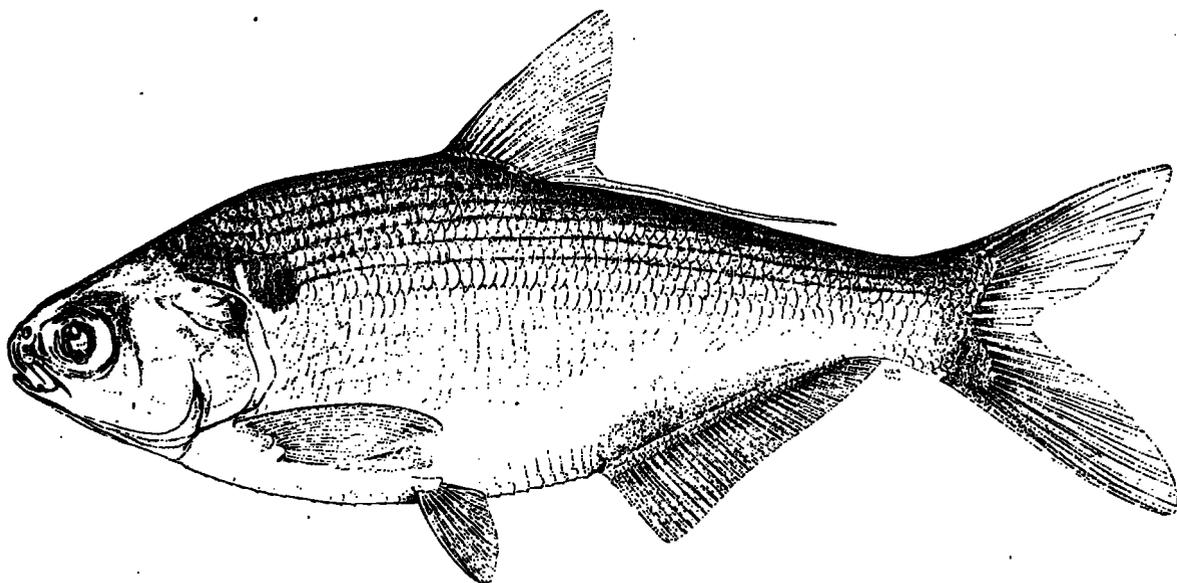


FIGURE 1.—Adult female *Dorosoma cepedianum* (UMMZ 128171), 180 mm. standard length (about 9 inches total length), from Lafayette County, Arkansas. (Drawn by W. L. Brudon.)

20–65 mm., about 350 at 95 mm., and 412 in a specimen 157 mm. long.

Although the adult (fig. 1) is a deep-bodied, strongly compressed fish, the young (fig. 4, *c*) is slender, minnowlike, and nearly cylindrical. The maxillaries on young specimens have a few minute teeth on the lower edge which are lost with age. The highly specialized digestive tract of the adult is also lacking in the young, which have an almost straight intestine and no pyloric caeca. By the end of the first summer, however, the young possess the specializations of the adult.

No external characteristics will reliably distinguish the sexes.

Color.—In life the body is silvery bluish over the back and upper sides but milky white on the abdomen, and often has brassy or golden reflections from the scales. There are six to eight horizontal, dark stripes along the upper sides above the level of the middle of the shoulder spot, extending from behind the head to the base of the caudal fin. The large, round dark spot behind the opercle, so prominent in the young and half-grown, is lustrous purple. In adults, the dorsal fin is nearly uniformly dusky; the caudal fin is dusky but darkened on its outer third; the outer two-thirds of the anal fin is dark, the basal third lighter, with melanophores sprinkled over most of the fin; the pectorals and pelvics have their outer halves darkened, paling basally. The top of the head, snout, upper jaw, and upper part of the opercle are pigmented in young and adult; the rest of the head is silvery. In young-of-the-year (up to about 4.5 inches, total length), the dorsal fin is sparsely but uniformly sprinkled with chromatophores; the caudal fin is similar but has more pigment cells; the anal, pectoral, and pelvic fins are almost unpigmented. A good color plate of the species is given by Forbes and Richardson (1920, opposite p. 46).

Variation.—Insufficient data concerning certain variations in this species led to the recognition of at least three nominal subspecies; namely, *D. c. cepedianum* (LeSueur), on the Atlantic slope southward and westward along the Gulf of Mexico; *D. c. heterurum* (Rafinesque), in the middle and upper parts of the Mississippi River system and the Great Lakes–St. Lawrence watershed; and *D. c. exile* Jordan and Gilbert, in coastal streams from Texas to northeastern México. As Jordan (1882: 871) stated, "The

difference between *heterurum* and *cepedianum* is not great, the greater arch of the back in *cepedianum* being the main difference." It was soon recognized that this minor feature does not characterize these inland populations of gizzard shad. The form described from Texas (Galveston) has persisted much longer in the literature (e.g., Fowler 1945: 22, 366). This nominal subspecies, very briefly and inadequately described, was based solely on the supposedly slenderer body (body depth about 2.9–3.3, rather than 2.5–2.7 in specimens from Indiana and South Carolina), whence the Latin word *exile*, meaning slender. Unfortunately, the two type specimens (USNM No. 30913) have not been found. Although I have not examined specimens from Galveston, the ratios of body depth to standard length (table 1) demonstrate that subspecies of *Dorosoma cepedianum* cannot be recognized on this basis.

TABLE 1.—Variation in body depth in regional samples of *Dorosoma cepedianum*

Area	Range in standard length (mm.)	Ratio	Average	Number of specimens
Maryland to North Carolina.....	61–211	2.3–2.95	2.65	26
Middle and upper Mississippi R.—Great Lakes systems.....	78–215	2.35–2.85	2.62	38
Western Florida to Louisiana.....	84–204	2.5–3.1	2.69	20
Texas.....	56–196	2.45–2.9	2.69	29
Northeastern Mexico.....	81–227	2.4–2.9	2.68	12

NOTE.—The depth was stepped into the standard length by using fine dividers under magnification.

The dark shoulder spot (fig. 1) is said to disappear with age but is variably developed in different populations. This spot, present in young and half-grown, is typically seen in small adults and frequently in large ones. For example, the nominal species *Chatoessus insociabilis* Abbott was based in part on the retention of this marking in large adults. This spot was well developed in a freshly preserved series of adults, 165 to 204 mm. in standard length, from the Escambia River, Florida.

Study material.—The proportions used in the description are based on 74 specimens, between 78 and 247 mm. standard length, representing localities in Florida, Alabama, Mississippi, Louisiana, Texas, and northeastern México, and from Oklahoma, Arkansas, Tennessee, Missouri, Kansas, Nebraska, Iowa, Illinois, Indiana, Ohio, and Michigan. Specimens from Atlantic coastal waters

are not represented in the general description, but they were used in a study of variation in body depth. Counts of fin rays, scales, and ventral scutes are based on 51 to 200 specimens distributed from Michigan and Maryland southward and westward to Tamaulipas, San Luis Potosí, and Querétaro, México. Vertebral counts are based on 42 specimens from localities scattered over the range of the species.

Reproduction and development.—Spawning takes place in fresh water (Gunter 1938: 71) from late winter (mid-March) through most of the summer (at least to August 20) in sloughs, ponds, lakes, and large rivers. A group of males and females swimming near the surface begin to roll and tumble about each other in a mass, the eggs and sperm being ejected during this activity. The sticky eggs slowly sink to the bottom or drift with the current, readily becoming attached to any object they may contact. At times the small eggs cover aquatic vegetation, particularly streamers of green algae adhering to rocks, forcing the plants to the bottom of the pond or river. Gizzard shad generally spawn on a rising temperature although on one occasion Trautman (personal communication) found them spawning on a falling temperature at Buckeye Lake, Ohio. Langlois (1954: 224) observed gizzard shad spawning along shore, at a depth of 6 to 12 inches, on May 29, 1935, in North Reservoir, Akron, Ohio; when oviposition occurred (67° F.) a female was flanked on each side by a male.

The bulk of the populations that inhabit the warm to temperate waters of the United States (28° to 41° N. Lat.), spawns during April, May, and June at temperatures between about 50° and 70° F., the onset of spawning varying with the season. For example, in experimental ponds at Auburn, Ala., gizzard shad hatched at the end of April in 1941 but first appeared in the middle of March in 1942; in 1941 the last brood hatched on August 20 but in 1942 hatching continued only into July (Swingle 1949: 53). In Chickamauga Reservoir on the Tennessee River, a few miles above Chattanooga, Tenn., most individuals had spawned by the last week of May in 1942; all adults examined on June 9–10 had spawned, about two-thirds of the females studied June 1–5 were spent, and very few adults had spawned prior to May 22 (Eschmeyer, Stroud, and Jones, 1944: 96). In Norris Reservoir, Tenn., shad

spawned in 1943 between May 18 and June 8, when surface temperatures varied from 73.5° to 81.7° F.; in 1944 most of the spawning took place between May 15 and June 1, with the temperature from 78° to 84° F. (Dendy 1946b: 121). Gonads were ripening near the end of January 1954 in Lake Panasoffkee, Fla., with the bulk of spawning taking place in March and April and completed in May (Moody 1957: 30, 38). Near the northern limit of its range, in Fort Randall Reservoir, S. Dak., all adults caught after July 6, 1955, had spawned and most of those obtained before June 24 were green, indicating a short and comparatively late spawning period (Shields 1956: 30). Bodola³ found that water temperature during development of the eggs is probably more influential in determining the time of peak spawning than is the water temperature immediately preceding the spawning period.

At Buckeye Lake, Ohio, a shallow impoundment in the Ohio canal system, the gizzard shad begins to spawn when the water warms to 60° F., usually during the first part of May but varying from year to year. The spawning period normally extends over about 2 weeks, with an occasional ripe female found later in the season (one was taken in the latter part of July) (Warner 1941: 639; observations made 1938–40).

In Iowa, the species is reported to spawn in late April or early May (Harlan and Speaker, 1956: 60). In the vicinity of Greenwood, Miss., a gravid female was taken in June 1925 (Hildebrand and Towers, 1928: 114). In Chesapeake Bay, Md., the gizzard shad spawns in "early summer" (Hildebrand and Schroeder, 1928: 107). Ripe males and females were recorded from the central part of the Illinois River, Ill., during May (Forbes and Richardson, 1920: 47). A spring spawning migration (dates not given) up the Mississippi River is reported by Gowanloch (1933: 215).

The embryology and early life history of the gizzard shad have been studied by Edward N. Warner, and reported in abstract (Warner 1941). Dr. Warner has kindly permitted me to use material from his doctoral thesis that did not appear in the abstract, including drawings of the embryonic and larval stages (figs. 2–4).

³ Bodola, Anthony. The life history of the gizzard shad, *Dorosoma cepedianum* (LeSueur), in western Lake Erie. Ph.D. thesis. Ohio State University. 1955: i-xi, 1-130, figs. 1-44.

The nearly transparent, fertilized egg measures about 0.75 mm. in diameter after fixation. When first extruded, it is irregular and wrinkled but soon becomes spherical in the water; it is creamy yellow as seen under the microscope. There is no perivitelline space between the enclosing capsule and the egg, which is not free to turn. There is a heavy adhesive layer around the outside pierced by a micropyle. The newly laid egg sticks to any object it contacts. The yolk consists of closely packed, slightly granular globules, and there is one large clear oil globule and one or two (rarely 3 to 5) smaller ones.

Shortly after fertilization (15–20 minutes at 80° F.), the cytoplasm becomes raised at one side of the yolk to form a single blastomere. After about an hour of incubation (80° F.), the first cleavage furrow is complete, bisecting the blastomere. During the early cleavage stages and later, the egg of this species follows a course that is typical of teleostean development.

The embryo (fig. 2, *a* to *f*; fig. 3, *a* and *b*) hatches after 95 hours of incubation at 62° F. (or about 36 hours at 80° F.), and a continuous fin is formed around the posterior two-thirds of the body (fig. 3, *c*). Bodola (*see* footnote 3) found the hatching time varied from about 36 hours to approximately 1 week, depending on water temperature. The prolarva⁴ (fig. 3, *c-e*) immediately sinks toward the bottom, head downward. After sinking a few inches, swimming movements orient the head region upward and the prolarva continues to swim upward for about the same distance that it sank. Such alternate sinking and rising movements characterize the behavior of the gizzard shad for the first 2 days after hatching. The average total length of the prolarva is 3.25 mm., its body depth (including finfold) 0.2 mm.; the length of the yolk sac is 0.8 mm. There are about 32 pairs of somites. At this stage the small fish is so transparent that it is seen only with difficulty in a jar of water. The unpigmented eyes are fairly well-developed and possess a lens, but a wide choroid fissure persists. The conspicuous auditory pits lie a short distance back of and slightly above the eyes. The head is flexed downward at an angle of 90° and is joined to the anterior margin of the yolk sac. The hind gut lies outside of the body wall proper and

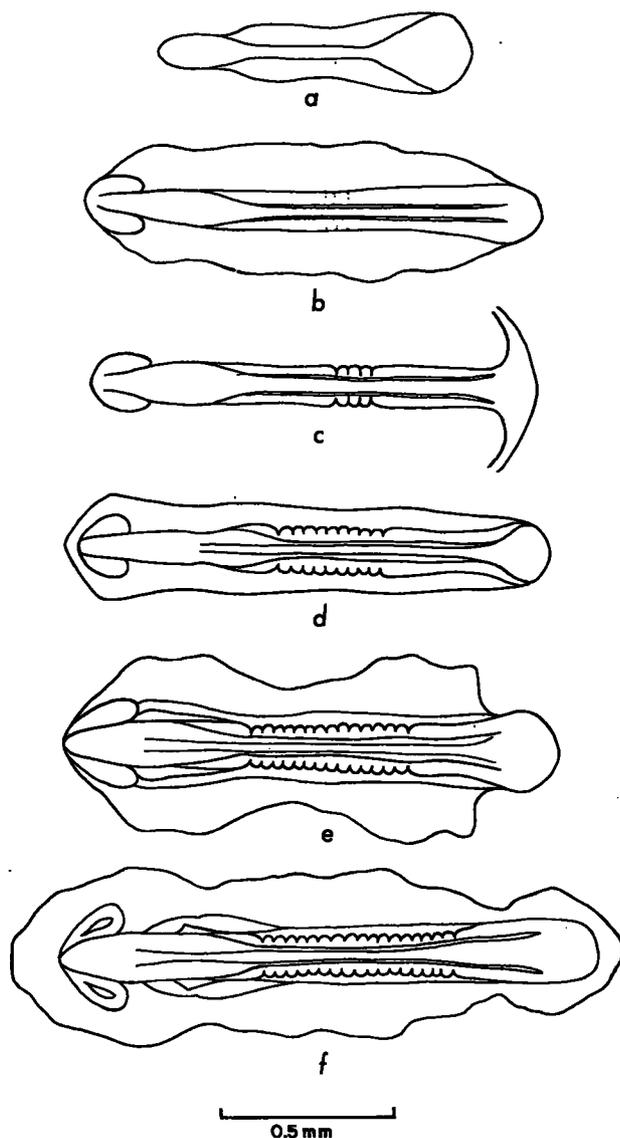


FIGURE 2.—Embryonic development of gizzard shad at various stages after fertilization at a water temperature of 62° F. *a*, Early embryo, 27 hours; *b*, embryo of 2 somites, 33 hours; *c*, embryo of 3 somites, 38 hours; *d*, embryo of 9 somites, 43 hours; *e*, embryo of 14 somites, 48 hours; *f*, embryo of 17 somites, 52 hours.

extends posteriorly to the level of the last somite, where it turns downward and ends in the vent at the margin of the finfold.

The 1-day-old prolarva (fig. 3, *d*) averages about 5.5 mm. total length. The head has lost its distinct downward flexure, and the heart is now pulsating although there is no pigmented blood. The oral plate on the ventral surface of the head is perforated but the pharynx is not open

⁴I follow the terminology recommended by Hubbs (1944).

into the mouth cavity. The choroid fissure of the eye is closed, and the anlagen of the pectoral fins are evident in the form of small rounded buds. There is still no pigmentation, most of the yolk sac is absorbed, and there are about 40 myotomes.

The 3-day-old prolarva (fig. 3, *e*) is about 6.5 mm. long. The cartilage of the lower jaw is now forming and there are four gill arches but no gill filaments. The pectorals are small, paddle-like appendages and only a vestige of the yolk sac remains. The alimentary canal appears to be complete. There is a row of conspicuous chromatophores on each side of the body along the

roof of the alimentary canal dorsal to the yolk sac. A row of pigment cells also occurs along the base of the finfold, from the yolk sac to the vent. The vent is close to the body, in a notch at the base of the finfold.

Subsequent stages (postlarval, fig. 4, *a-c*) were obtained from Buckeye Lake, hence their ages are unknown. Development beyond the 3-day stage consists primarily of growth in length and depth and the gradual acquisition of adult characteristics. The dorsal, caudal, pectoral, pelvic, and anal fins develop in the sequence named. The internal folds of the intestine develop (seen in a 10.8-mm specimen, fig. 4, *a*) and the operculum

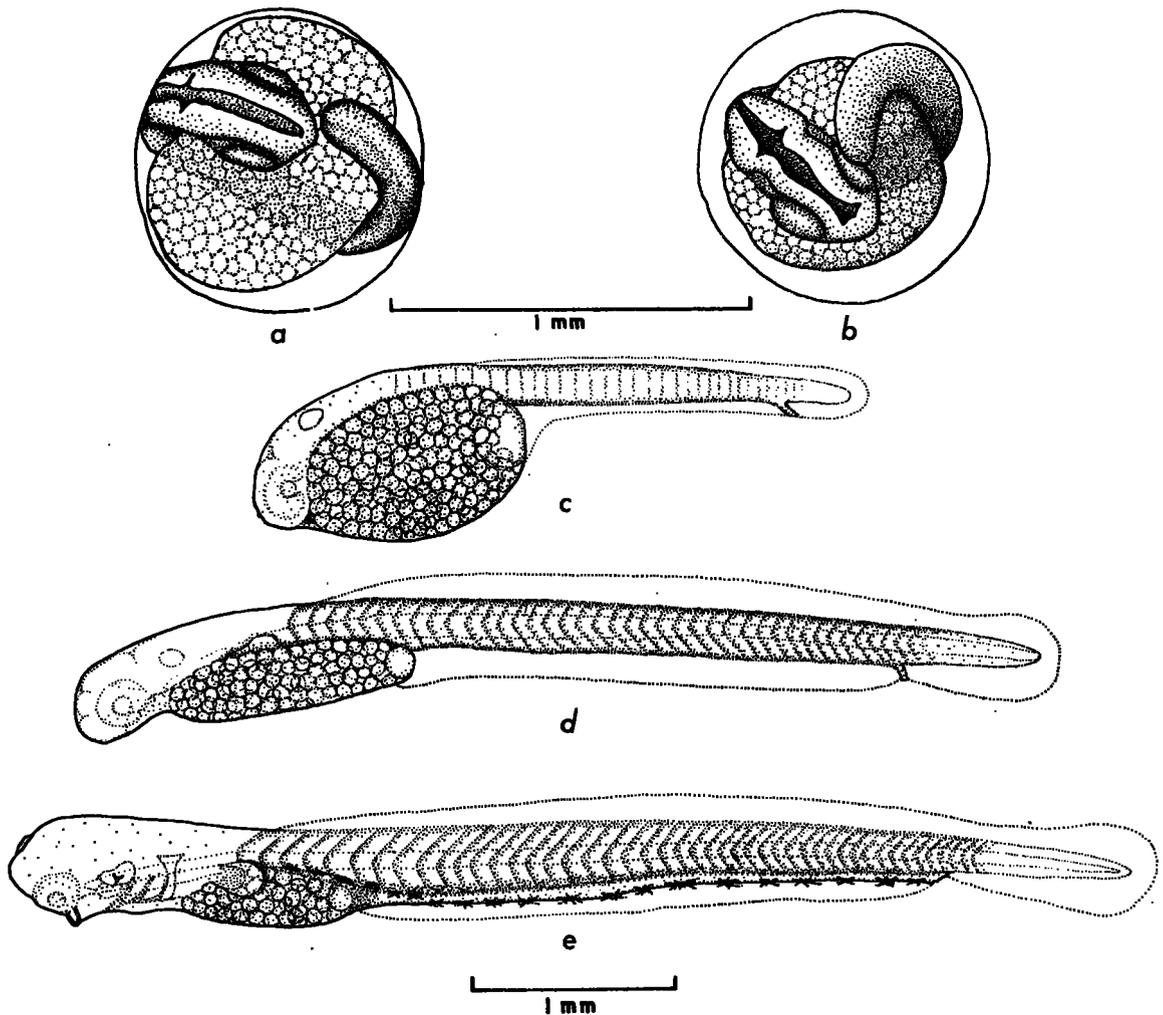


FIGURE 3.—Embryonic and larval development of gizzard shad at various stages after fertilization at a water temperature of 62° F. *a*, Complete circle of yolk, 60 hours; *b*, advanced embryo, 70 hours; *c*, hatching stage, 32 somites, 95 hours; *d*, 1-day-old larva in finfold stage, 119 hours; *e*, 3-day-old larva in primary pigmentation stage, 162 hours.

grows posteriorly to cover the gills. The auditory pit becomes invisible from the surface by the overgrowth of the head skeleton and musculature. The pigmentation becomes more prominent, especially along the dorsal surface and on the dorsal and caudal fins. Bodola (*see footnote 3*) was unable to rear the young beyond the 10th day after hatching, at which time his fry were slightly more than 6 mm. long.

The larvae of the gizzard shad may be distinguished from those of fishes with which they may be confused by the long gut (1.5 to 2.0 times the total length of the fish), the retarded development of the single dorsal fin, and the elongated anal fin (22 rudimentary rays at 17.5 mm., 30 to 34 at 10 to 22 mm. total length).

Fecundity.—In his study of the gizzard shad in Lake Erie, Bodola (*see footnote 3*) found considerable variation in the estimated number of eggs per individual female. Two females of age-group I, averaging 231 mm. in standard length, had an average of 59,480 eggs; 5 females of age-group II, 291 mm. long, averaged 378,990 eggs; 3 individuals of age-group III, averaging 331 mm. long, had 344,780 eggs; 2 in age-group IV, 356 mm., averaged 308,750; and 1 female of age-group VI, 355 mm. long, had an estimated 215,330 eggs. Although meager, the data show that precocious shad have few eggs, that the II-group individuals have the most eggs, and that egg production declines with successively older groups. Fish weighing between 500 and 600 grams

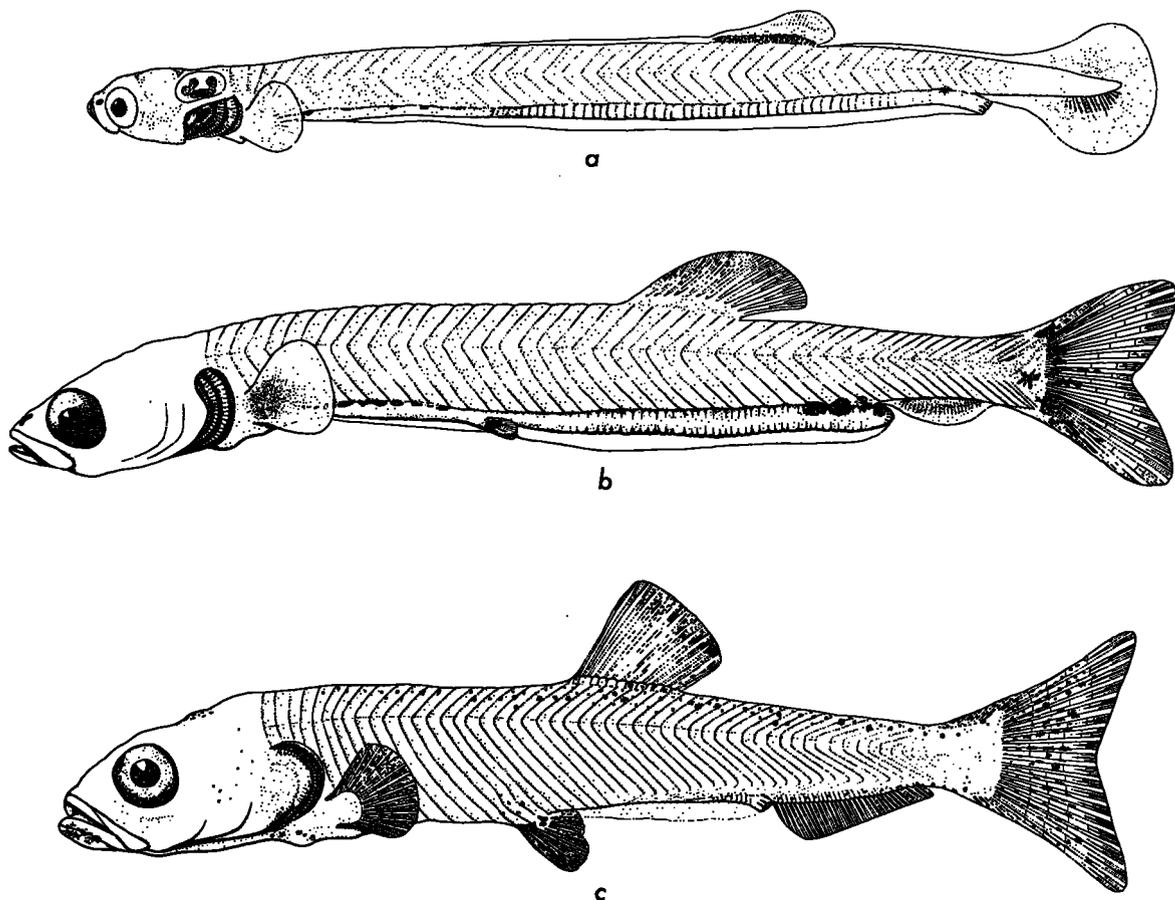


FIGURE 4.—Larval development of gizzard shad collected in plankton net, Buckeye Lake, Ohio. *a*, Eye-pigment stage, length 10.8 mm., age unknown; *b*, pelvic-fin stage, 17.5 mm., age unknown; *c*, definitive-fin stage, 22.0 mm., age unknown.

produce the most eggs. A ripe female 315 mm. long, taken in June 1925, near Greenwood, Miss., contained approximately 50,000 eggs according to Hildebrand and Towers (1928: 114).

Age and growth.—Data on the age and growth of the gizzard shad have been summarized recently by Carlander (1950: 24–25; 1953: 282–283) and further treated by subsequent authors. The following summary is taken in large part from the original papers cited therein.

In Foots Pond, Ind., growth of young-of-the-year, as noted in samples taken on four successive dates in 1940, was as follows (standard length range, in mm., followed by average length): 19.0–44.5, 31.4 (71 specimens, June 26); 32.0–65.0, 57.0 (29, July 10); 45.0–79.0, 66.6 (42, August 20); and 61.0–88.0, 72.4 (70, November 13). Growth is very rapid in the first 5 to 6 weeks of life and gradually tapers off as the season progresses (Lagler and Applegate, 1943: 104–105). At the end of the first summer, an average total length of about 4 inches is attained (Indiana and Ohio); total length is about 4.5 inches in the Chesapeake Bay region, and 5.0 inches in Tennessee and Oklahoma.

A summary of the age and growth of *Dorosoma* in Foots Pond and Grassy Pond, Ind., as determined from samples collected between June 26 and August 28, 1940, is given in table 2. Studies on gizzard shad from the Chickamauga Reservoir, Tenn., in 1942, showed that 1-year-old fish had a modal length of 7 inches in June and about 7.5 inches by fall; 2-year-old fish were about 8.5 inches long in April; and the largest shad were about 16 inches long. Young shad (born in late May or early June) showed an average length of approximately 1.5 inches by the last week in June, 2.5 inches by mid-August, and 3.5 inches by late September (table 3). A summary of growth in Grand Lake, Okla., over a 13-year period (Jenkins 1953a: 53), showed that here, as at Herrington Lake, Ky., first-year growth is only about 4.5 (rather than 7) inches, thus extending the time during which gizzard shad are available as a forage fish. The average length of gizzard shad in Crab Orchard Lake, an artificial impoundment in southern Illinois, was only 4.0 inches at the end of the first year, 5.4 inches at the second year, and 6.6 inches at the end of the third year (Lewis 1953).

TABLE 2.—Age of gizzard shad and average lengths of fish in each age group in two Indiana ponds, June 26–August 28, 1940

[From Lagler and Applegate, 1943: table 3]

Item	Age group ¹					
	0	I	II	III	IV	V
Number of specimens.....	242	38	84	81	25	6
Size range (mm.).....	19–79	130–180	172–222	180–238	199–250	230–309
Size range (in.).....		7–9	9–11	9–12	10–13	11–15
Average standard length (mm.).....	41	152	193	207	223	256
Average total length (in.).....		7.6	9.7	10.5	11.3	12.8

¹ Based on number of annuli.

TABLE 3.—Length distribution of 11,240 young-of-the-year gizzard shad in Chickamauga Reservoir, Tenn., 1942

[From Eschmeyer, Stroud, and Jones, 1944: table 14]

Total length (mm.)	June 24–30 ¹	July 6–21 ²	August 3–20 ³	September 2	September 28–29	October 27
21–26.....	123	7				
27–32.....	202	26				
33–38.....	366	509	1			
39–44.....	546	767	10			
45–50.....	336	269	58			
51–56.....	221	213	126	11		
57–62.....	207	187	154	31	22	1
63–68.....	123	115	157	183	163	3
69–74.....	74	122	165	464	256	22
75–80.....	27	166	135	478	297	92
81–86.....	7	105	129	336	481	224
87–92.....		44	77	161	604	362
93–98.....	1	11	59	112	437	214
99–104.....		3	26	53	118	76
105–110.....		2	13	11	52	31
111–116.....			2	4	11	18
117–122.....			1		4	7
123–128.....				2	4	4
129.....				1		1
Total.....	2,233	2,546	1,113	1,847	2,446	1,055

¹ Five samples collected on June 16, 24 (3 samples), and 30.

² Four of the six samples taken were collected on July 7.

³ Four collections made on August 3, 12, 19, and 20.

At the end of the first year of life in Fort Randall Reservoir, S. Dak., the average total length of the 1954 age group was 5.1 inches (170 specimens) and of the 1953 age group 7.0 inches (Shields 1956: 30). Somewhat greater average lengths are given for samples from Black River, Mo., by Patriarche and Lowry (1953: 99–105).

The gizzard shad typically matures in its second or third year and lives for at least 7 years, in Oklahoma (Jenkins 1953a: 54) and Lake Erie (Bodola; see footnote 3, p. 376). Patriarche (1953: 249) found 10-year-old gizzard shad in Lake Wappapello, Mo., but stated that in other Missouri reservoirs the species lives no longer than 5 or 6 years. Gizzard shad in Lake Newnan, Fla., average about 10 inches (total length) at the end of their first year of life, about 12.5 inches at the end of the second year, and about 13.6 inches at

the completion of the third year—thus indicating rapid growth coupled with a very short life span. Only about 5 percent approach their third actual year of life and none over 4 years old was found (Berry 1958).

From 70 to 80 percent of the annual growth of gizzard shad in Lake Erie takes place during June, July, and August or July, August, and September, depending on the season and the age of the fish. The species grows little if at all during winter, when considerable loss of weight occurs (Bodola; *see* footnote 3).

There was no sexual dimorphism in the rate of growth or in the length-weight relation for 1,136 gizzard shad from Beaver Dam Lake, Ill. (Lagler and Van Meter, 1951: 357-360).

Abnormal growth has been reported by Hubbs and Whitlock (1929), who found two extreme forms in samples taken not far apart in the Arkansas and Poteau Rivers, Okla. The abnormal sample, composed only of young fish, showed a teratological condition (head long, wide, and swollen; eyes large; tails stunted) that was evidently related to an environmental factor or factors.

Size.—The gizzard shad is known to attain a total length of 20.5 inches but does not commonly grow longer than 10 to 14 inches. In a letter dated July 14, 1953, Alfred Larsen (Fishery Biologist, Pennsylvania Fish Commission) wrote that specimens of *Dorosoma cepedianum* killed in Presque Isle Bay early in 1953 (*see* section on Mortality) varied in length from 4 to 19 inches. Maturity may be attained at much smaller sizes than commonly thought, for Vladikov (1945: 35) reported a mature female to be 151 mm. (a little over 6 inches) in total length. Fish 10 to 13 inches long weigh about 1 pound; individuals 14 to 18 inches long, from the Ohio River drainage of Ohio, weigh 1 to 3 pounds; and the largest recorded specimen (20.5 inches) weighed 3 pounds 7 ounces (Trautman 1957: 182). As in other fishes, size and weight vary considerably and in some localities there is marked dwarfing.

Habitat and migration.—The gizzard shad inhabits large rivers, reservoirs, lakes, swamps, bays, borrow pits, bayous, estuaries, temporary floodwater pools along large river courses, sloughs, and similar quiet open waters which may be clear to very silty. Although it is fairly

common in the relatively strong current of the upper Mississippi River, it prefers quieter waters and swarms in the sluggish lower parts of the same river. The adults may ascend smaller streams or ditches to spawn and the young are later abundant in such places if the gradient is sufficiently low. In coastal rivers of Virginia the young are present in great abundance well upstream from brackish water (Massmann 1953). In Lake Erie the species is most plentiful at the shallow western end, over mud bottom (Nash 1950: 563), particularly in protected bays and about the mouths of tributaries (Bodola; *see* footnote 3). Abundance is greatest in late summer and early fall when the populations are augmented by young-of-the-year. The species is particularly attracted by warm water flowing from industrial plants (*see* section on Mortality). It is able to withstand rather high temperatures, to 35° C., and has shown no geographic variation in its ability to tolerate lethal temperatures (Hart 1952: 28-29).

Gizzard shad are common in Chesapeake Bay only during the fall months, occurring principally in brackish water near the mouths of freshwater streams. The species is common or abundant in the rivers of the region throughout the year, but very young individuals evidently do not enter brackish water (Hildebrand and Schroeder, 1928: 106-108). Along the Texas coast, the species frequents the large, brackish-water bays where individuals may be taken throughout the year in waters that vary in salinity from 2.0 to 33.7 parts per thousand. Gizzard shad in this area prefer brackish water to sea water and, in general, the smallest fish occur in the freshest water, with size increasing as salinity increases (Gunter 1945: 30-31).

Dorosoma cepedianum is essentially an open-water species, usually living at or near the surface, and the young are reported to prefer beds of spatterdock (*Nuphar*) in Fouts Pond, Indiana (Hubbs and Lagler, 1943: 77). In western Lake Erie, young shad live close to shore in mid-summer, usually in shallow water (Bodola; *see* footnote 3). If the oxygen supply is adequate, the species may descend to depths as great as 108 feet, as in Norris Reservoir, Tenn. (Cady 1945: 113-114; Dendy 1945: 126; 1946a). In the Coosa River, Ala., gizzard shad were found in deep (25

feet) as well as shallow water (Scott 1951: 38-39).

Young-of-the-year gizzard shad travel in compact schools soon after hatching, but by fall most of the schools disperse and few form the following spring, at least in Norris Reservoir; schooling largely ceases by the time the shad are a year old (Dendy 1946b: 121). In the Chesapeake Bay region there is a fall "run" in September and October, and a corresponding spring "run" has been recorded in North Carolina. A spring migration, evidently a spawning run, has been noted in the Mississippi River near New Orleans, and lake populations migrate to shallower water at spawning time. An unusual mid-winter migration was noted in the Minnesota River, from about December 1 until late January (Swanson 1932: 34).

Food.—Except for a short time after hatching, this species is almost entirely herbivorous, feeding heavily on microscopic plant life, phytoplankton, and algae.

At birth the alimentary canal is a simple, nearly straight tube (fig. 4, *a*) but by the time the wild fish is about 22 mm. long four flexures have developed; the section between the first and second flexures subsequently enlarges to become the gizzard and caeca arise from the duodenum by the 27.5-millimeter stage. The intestine becomes tremendously convoluted with age; whereas it equals about one-half the total length of the day-old fish, it becomes three times the length of the adult and is packed into an abdominal cavity only one-third that of the fish's length. The young commence to eat about 4 or 5 days after birth (Bodola; *see* footnote 3). Wier and Churchill (1946) have described the anatomy and histology of the digestive system.

During the first few weeks of life, gizzard shad eat mainly protozoa and entomostraca. Contents of the digestive tracts of larval and postlarval shad examined by Warner (*see* Wickliff 1945: 1-4) consisted almost entirely of water fleas (*Bosmina*), copepods, and a few ostracods. These organisms were found in young up to about 22 mm. long. Individuals 26 mm. long, with the intestine, gizzard, and liver well developed and having essentially the appearance of the adult, contained largely algal plankton (diatoms, desmids, and colonial forms) and shelled and flagel-

lated protozoa (*Euglena*), which occur in the bottom ooze, on vegetation and as free-floating organisms. At this size, *Bosmina* has almost disappeared from the diet. Food may occur in the pharyngeal pockets, the gizzard, and the intestine (Bodola; *see* footnote 3).

The algal consumption of the gizzard shad led Tiffany (1922: 285) to describe these fish as "living tow nets." He identified 150 species and varieties of nonfilamentous algae from the stomach and intestine of specimens taken in streams and ponds of Ohio and Illinois. To what extent these are utilized as food is questionable, however, for Velasquez (1939) showed experimentally that 50 of the above species might have been viable after passing through the digestive tract. A certain amount of mud is typically ingested by the shad while feeding (hence the name, mud shad), but this material is evidently taken accidentally; however, sand may be purposefully ingested as an aid in the macerating action of the gizzard (Bodola; *see* footnote 3). On occasion, the species may be cannibalistic (Dendy 1946b: 119).

Earlier Tiffany (1921: 383) gave a summary of the food eaten by young shad in six Ohio lakes. This consisted of microalgae, 70 to 90 percent; microanimals, 0 to 15 percent; filamentous algae, 0 to 5 percent; and plant debris, 5 to 20 percent. Mud usually comprised from 10 to 30 percent of the stomach and intestinal contents, but it was often absent. The gizzard shad is able to utilize a large variety of microscopic plants and it does so consistently. Moreover, the diet is remarkably alike at various sizes (once the early zooplankton stage is passed). Tiffany found that the percentage composition of food eaten by shad 200 mm. long was not materially different from the data given above for young fish, except that there was more unrecognizable debris. Examination of intestinal contents in samples from Lake Erie showed that little food is eaten in winter and early spring (Bodola; *see* footnote 3).

In the vicinity of distilleries this species will feed on distillery slops (cornmeal) and it may also occasionally take Coleoptera, univalve mollusks, young *Corixa*, and spiders and water mites (Forbes 1888: 438; Forbes and Richardson, 1920: 47).

Seven specimens from Buckeye Lake, Ohio, 22 to 31 mm. in total length, taken on June 25 and July 11, 1930, yielded 14 percent Cladocera and 86 percent algae and debris (Ewers and Boesel, 1936: 61). Some of these individuals were in the transitional stage during which zooplankton is being replaced by phytoplankton in their diet.

Predators.—At a certain stage in its life history, the gizzard shad is reported to form a major part of the diet of at least 17 important game fishes. Of value in this respect are young-of-the-year about 2 to 5 inches long, but individuals 8 inches or longer are utilized to some extent by walleyes (*Stizostedion vitreum*), according to Stroud (1949). In ponds and lakes of Ohio, it is preyed upon by white bass (*Roccus chrysops*), largemouth bass (*Micropterus salmoides*), and white crappie (*Pomoxis annularis*) (Wickliff and Trautman, 1931: 15, 25, 37). In Foots Pond, Ind., the gizzard shad was eaten by three gars (*Lepisosteus platostomus*, *L. productus*, and *L. osseus*), white bass, largemouth bass, white crappie, and black crappie (*Pomoxis nigromaculatus*), according to Lagler, Obrecht, and Harry (1943: 120, 122–123, 126), and Lagler and Ricker (1943: 59–62). Two gars, *L. productus* and *L. osseus*, utilized the species in Texas (Bonham 1941: 359–360), and the skipjack (*Alosa chrysochloris*), northern pike (*Esox lucius*), yellow bullhead (*Ictalurus natalis*), and white crappie preyed upon the gizzard shad in Illinois (Forbes 1888: 435; Hansen 1951: 225). In the Illinois River, Forbes (1903: 34–38, 40) reported that walleye (*Stizostedion vitreum*), sauger (*Stizostedion canadense*), and yellow bass (*Roccus interruptus*) preyed upon shad between 3 and 4 inches long and that this species was a very important item in their diet.

In Norris Reservoir, Tenn., Dendy (1946b: 122, 124) stated that *D. cepedianum* constitutes the most important food supply for the game fishes. These are channel catfish (*Ictalurus punctatus*), largemouth bass, smallmouth bass (*Micropterus dolomieu*), spotted bass (*M. punctulatus*), black crappie, walleye, sauger, and the freshwater drum (*Aplodinotus grunniens*). In the Clinch River, Tenn., white bass and largemouth bass fed mostly on gizzard shad and brook silversides (Eschmeyer 1944: 38).

Even the lake trout (*Salvelinus namaycush*) is credited with eating *Dorosoma* in Cayuga Lake, New York. An examination of 312 stomachs that contained food revealed one with a gizzard shad 6.7 inches long.⁵ The bowfin, *Amia calva*, also is known to eat gizzard shad (Lagler and Hubbs, 1940).

The periodic mortality (see elsewhere) of gizzard shad provides an important source of food for numerous species of waterfowl. This food comes at a most opportune time, when other foods are scarce or when waterfowl are forced out of their normal feeding places by hunters. Young-of-the-year shad are fed upon at Buckeye Lake, Ohio, during the fall and winter by the lesser loon, horned grebe, pied-billed grebe, white pelican, great blue heron, American egret, snowy egret, eastern green heron, black-crowned night heron, American merganser, red-breasted merganser, hooded merganser, mallard, black duck, gadwall, baldpate, green-winged teal, blue-winged teal, American pintail, wood duck, redhead, canvasback, lesser scaup, ring-necked duck, American goldeneye, bufflehead, oldsquaw, king eider, American scoter, and whitewinged scoter (Trautman 1940: 110–111, 155–206). During the relatively open winter of 1952–53 at Columbus, Ohio, Trautman (personal communication) stated that the huge waterfowl concentrations in central Ohio would have been impossible without the gizzard shad.

Utilization.—The gizzard shad is not esteemed for food by man because of its soft and rather tasteless flesh and the numerous fine bones. There is no evidence that the aborigines sought this species (Rostlund 1952: 14). In the Chesapeake Bay region it once sold fairly well to a class of trade that demanded a cheap fish. In 1921, the retail price in Baltimore was about 5 cents a pound. Among the commercial fishes of Chesapeake Bay in 1920, it ranked twentieth in value with a catch of 72,852 pounds worth \$2,013 (Hildebrand and Schroeder, 1928: 107). The commercial catch in the Great Lakes over a 14-year period (table 4) shows the erratic nature of the take.

⁵ Galligan, James P. The distribution of lake trout and associated species in Cayuga Lake. M.A. thesis, Cornell University, 1951: 72.

TABLE 4.—Commercial catch of *Dorosoma cepedianum* in the Great Lakes, 1939–57

[Excluding Lake Superior. From statistical records of U.S. Fish and Wildlife Service and Michigan Department of Conservation]

Year	Lakes	Pounds ¹	Value ¹
1939	Huron	300	\$18.00
1940	Erie, Huron	35	1.00
1941	Huron	300	6.00
1942	Erie (Pa.)	23,000	139.00
1943	Erie, Huron	900	44.00
1944	do	300	13.00
1945	do	600	28.00
1946	Huron	100	7.00
1947	Erie, Huron	600	10.00
1948	Huron	29,400	294.00
1949	Erie, Huron	31,600	930.00
1950	do	20,600	614.00
1951	do	450	16.00
1952	do	2,300	55.00
1953	Huron	100	1.00
1954	Ontario, Erie, Huron	2,200	32.00
1955	Huron, Michigan	3,700	41.00
1956 ²	do	5,180	149.00
1957 ²	do	4,750	95.00
Total		126,415	2,493.00

¹ To nearest round figure.² For State of Michigan only; final figures for 1957 are approximate.

The species has been used to some extent in making guano, and in 1874 a guano factory existed at Black Point, above Palatka, Florida (Bean 1893: 64; Goode 1884: 610). Many years ago, on Lake Erie, it was split and salted and sporadically marketed with other low-grade fish as "lake shad" (Jordan 1882: 871), and in the 1840's it appeared on the markets in Ohio but was not highly regarded (Kirtland 1838: 195).

When it becomes excessively abundant, as it did in Black Hawk Lake, Iowa, in 1951, the gizzard shad may be used as hog food or for field fertilizer (Madden 1951: 185). In the Ohio waters of Lake Erie, the harvest is limited and is restricted to Sandusky Bay. Here one commercial drag seiner takes shad, carp, and goldfish for use as hog feed, and another drag seiner provides enough *Dorosoma* to freeze for trout food (letter from Robert Cummins, Jr., Sandusky, Ohio, June 26, 1953). In the Pennsylvania waters of Lake Erie, where shad mortality has been high in recent years, the species has been steamed and pressed for oil and the remainder used as cattle food. Gizzard shad roe has occasionally been marketed for food in Florida (Moody 1954: 147). Its use as food for fur animals has been investigated. Since the whole fish contains considerable amounts of the enzyme thiaminase, it must be cooked or fed in a special feeding schedule. Protein content of the whole fish is about 15 percent and fat content 12 percent, which is

comparatively high (U.S. Fish and Wildlife Service, 1956).

The species has had limited use as a bait fish. Evermann (1899: 308) claimed that gizzard shad were "of considerable importance as bait" in the Atchafalaya River, Miss., but Kuhne (1939: 25) stated that since it dies very easily it is an unsatisfactory bait minnow. According to T. H. Bean (1893: 64), the shad "has been very successfully kept in the aquarium * * *." It has also been successfully propagated in ponds as food for young bass.

Although the gizzard shad can hardly be classed as a sport fish it is taken occasionally by angling, as at Lake Chautauqua, Ill. A hook baited with an angleworm, a small minnow, or even an artificial fly, is attractive to the shad, and Abbott (1861: 366) stated that the fish afforded much sport to juvenile anglers in New Jersey.

Abundance.—In recent years, the gizzard shad has become a problem species wherever it has so increased that a detrimental affect is produced on other fishes. *Dorosoma* has inhabited Lake Erie for more than 100 years, yet its greatest abundance there has been attained since about 1950, according to commercial fisherman (Bodola: see footnote 3). Fluctuating but generally increasing numbers in the Great Lakes, especially Lake Huron and Lake Erie, is indicated by the commercial catch from 1939 to 1957 (table 4). In 1948, 3,000 pounds were taken in one seine haul in Lake Huron, and it was noted that the fish were being captured in record numbers after a 15-year lull in abundance (Ann Arbor News, Mich., December 1, 1948). Overpopulation is typically associated with manmade modification of the environment (Lagler and Van Meter, 1951).

In Carpenter Lake, Ky., during October 1954, 285 pounds of gizzard shad per acre were killed with rotenone in an impoundment of 70 acres having an average depth of 5 feet and a maximum depth of 11 feet; only about 50 pounds of shad per acre were anticipated (Bowers 1955). Among forage fishes, there was a phenomenal increase in abundance of gizzard shad in Clearwater Lake, Mo. The percentage composition rose from 2.0 in 1949 (1 year after impoundment) to 57.8 in 1950; large schools of shad were seen in 1950 throughout the lake (Martin and Campbell, 1953: 59). Since the species had spawned before the reservoir filled

in 1948, the tremendous increase in 1950 resulted largely from brood stock spawned in 1949.

Black Hawk Lake, Iowa, became so overpopulated with *Dorosoma* that the game fishes were suppressed by sheer weight of numbers of gizzard shad (Madden 1951). In 1934 there was a complete winter kill in this shallow, fertile lake of 957 acres; in 1939, 105 acres were dredged so as to avoid further severe winter mortality. The depth was 6 to 7 feet except in the dredged portion, which was 9 to 16 feet. The first gizzard shad was netted in 1945 and by 1947 (when the lake was flooded by Boyer River) the population had reached a nuisance level. With the progressive increase of shad it was noted that bottom organisms declined. In the fall and winter of 1950-51, 10,000 adult *Dorosoma* were removed by seining. Largemouth bass, walleye, and northern pike were stocked in 1951 to provide predators to keep the shad in check, but in the fall of 1951 approximately 7,360 young gizzard shad per acre were removed from the lake. Nevertheless, through intensive netting during the period 1951-57, the poundage percentage of gizzard shad removed per haul (mostly by a 2,500-foot seine) decreased from 98.1 to 2.8; at the same time the poundage percentage for carp increased from 1.8 to 96.3—thus suggesting that the ecological niche vacated by the shad was rapidly assumed by the carp (Rose 1957).

Increase of gizzard shad in 31,000-acre Lake Apopka, Fla., reached the point (sometime between 1950 and 1956) where this species constituted more than 80 percent of the total fish population (Heinen 1958). By means of selective treatment with rotenone, an estimated 3.5 million pounds of *Dorosoma* were killed (November 4, 1957) in the first of three projected applications. Past records indicated a marked decrease of sport fishing after 1950 and a change in the lake from clear water and large quantities of submerged vegetation to turbidity (from high plankton bloom) and sparse submerged plants. Similar overpopulations of gizzard shad have occurred in other Florida lakes. For example, in Newnans Lake, Alachua County, with 6,182 acres, an estimated 1 million pounds of shad were destroyed with rotenone (Melvin T. Huish, personal communication). In five of seven shallow Florida lakes studied by Moody (1954), gizzard shad and

gars constituted about 50 percent or more of the total weights of fishes obtained by large haul seines.

In comparing fish populations in two similar Oklahoma lakes, Jenkins (1957) demonstrated that the lake containing gizzard shad had an estimated standing crop of 1,043 pounds per acre and a weight of desirable-sized fish of 466 pounds per acre, whereas the lake lacking this species had an estimated standing crop of 655 pounds per acre of which 608 pounds comprised desirable-sized fish. The average coefficient of condition for six species of sunfishes in the two lakes showed that the lake without shad was above the State average, whereas that containing *Dorosoma* was well below the State average. This is indicative of direct competition between centrarchids and gizzard shad in small-lake populations.

Parasites.—This species appears to be usually free from attack by parasites, from which it is undoubtedly protected by its herbivorous food habits. Bangham and Hunter (1939: 396) examined 5 gizzard shad from Lake Erie and found an unidentified larval nematode in the intestine of one young specimen. Van Cleve found but two species of Acanthocephala in 300 gizzard shad, and Essex and Hunter reported no parasites in more than 100 individuals from the Rock and Mississippi rivers (as cited by Bangham and Hunter). In Buckeye Lake, Ohio, where gizzard shad are abundant, the young often carry a very heavy infestation of a myxosporidian which forms large white cysts in the body cavity. Each of 15 adult shad from the same lake were free of parasites, and 10 of 12 young carried many of the encysted sporozoans (Microsporidia) described above, often giving them a "potbellied" appearance (Bangham 1941).

Mortality.—Many gizzard shad die during the winter, frequently in great numbers (Wickliff 1953). This is a rather regular and often spectacular phenomenon and on occasion may lead to a health problem, as it did when more than 1,000 tons of dead and live *Dorosoma* were removed from Lake Erie at Erie, Pa., during January and February 1953 (Walsh 1953: 2-4, 5 figs.). The mass mortality, which occurred in Presque Isle Bay, was the greatest in a sequence of similar deaths that took place there during the decade 1943 to 1953. The bay contains two basins, East

and West, each of which has an area of about 15 acres, with a maximum depth of 8 to 10 feet. The pumping of water from the East Basin to the West Basin by an electric power company resulted in a discharge of warmed water into the West Basin at a rate greater than 100,000 gallons per minute. At the time of the mass deaths, water in the West Basin varied from 55 to 60° F., whereas that in the East Basin and the bay proper was only 34–35° F. Dissolved oxygen was not low and, with one exception, carbon dioxide levels were not unusual. The mortality occurred in the warmer West Basin and was clearly associated with high temperature. In 1950, the previous record year, 800 tons of shad were removed from the same basin (I am indebted to Alfred Larsen, Fishery Biologist, Pennsylvania Fish Commission, for most of the foregoing information).

The cause of such mortalities is not completely understood. It has been suggested that a marked difference between the carbon dioxide tension of the surface water and the carbon dioxide partial pressure of the air is a causal factor (Powers 1938: 279). This has been disputed, for example by Baker (1942: 48), and it is generally felt that abrupt temperature changes cause the mass deaths of this species (see also Agersborg 1930). This factor was noted more than 100 years ago by Kirtland (1844: 237), who described a mass mortality of *Dorosoma* in the Miami Canal, Ohio, after an abrupt warming following prolonged cold weather. Kirtland, however, did not realize that the deaths were probably a direct result of the sudden temperature rise, for he attributed the mortality to an inability of the species to withstand the colder, northern climate. That low temperature is a factor limiting the distribution of the gizzard shad, however, is evidenced by their absence from the upper parts of Lake Huron and Lake Michigan and all of Lake Superior (Miller 1957: 108). Also, large numbers of young shad were seen frozen in the ice throughout Fort Randall Reservoir, S. Dak., during the winter of 1955–56, a mortality plausibly attributed to cold temperature (Shields 1956: 29).

The possibility that a fungus disease may be locally responsible for deaths of gizzard shad (Trautman, *in* Clark 1942: 255; also suggested to me in personal communication by Dr. George W.

Bennett) seems to me to be more likely the result of secondary infection after the shad are weakened. Bangham and Hunter (1939: 396) and Bangham (1941: 442) suggested that a sporozoan parasite may kill many young gizzard shad during August and September in Buckeye Lake, Ohio. However, the shad that die are represented by several year classes, indicating that the causal factor (or factors) is not necessarily correlated with age.

The gregarious habits of this species and its predilection for quiet waters may also lead to mass mortality. From about November 11 to 13, in 1952, a large run of shad from the Detroit River up the intake pipe (diameter, 5 feet) of the Parke-Davis Company plant in Detroit led to the death, from mechanical causes, of an estimated 2 to 3 tons of *Dorosoma* of rather uniform size. The reduced current velocity of the intake, as compared with that in the river, is a plausible explanation for the migration (summarized from report in the files of the Institute for Fisheries Research, Michigan Department of Conservation).

There are two reports of apparent mass spawning mortality, both from Florida (Moody 1957: 30). A marked reduction of the population, without subsequent immediate recovery, occurred in April or May toward the end of the spawning season. A similar mortality took place in the threadfin shad (*D. petenense*) in Florida (Berry, Huish, and Moody, 1956).

Forage value.—Since the 1880's when its food and feeding habits were first studied by Forbes, the merits of the gizzard shad as a forage fish have been repeatedly emphasized. Its important qualifications are (1) direct utilization of phytoplankton; (2) a high reproductive capacity and abundance; (3) general freedom from parasites; (4) a rapid rate of growth; and (5) utilization as food by important game fishes. It has been spoken of as "the most efficient biologically of all the forage fishes" (Hubbs 1934: 57) because of the short and efficient link in its food chain that directly connects basic plant life with game fishes.

Thus, it might seem as if the gizzard shad could be called the ideal forage fish, but its suitability in this regard is affected by certain ecological conditions. Because of rapid growth to

a size not eaten by predators ample breeding stocks of *Dorosoma* are assured, but undue multiplication of these stocks may result in competition with the predators. The heavy populations of gizzard shad in some waters may be partially responsible for high turbidity and this may lead to a decrease in productivity of game fish (Thompson 1941: 211, 214). The great abundance of young shad may result in competition for food with the young of game fishes. Illustrations of how shad populations can mushroom in warm, shallow bodies of water that have a soft mud bottom, high turbidity, and relatively few predators have already been given (see section on Abundance, p. 384). Here *Dorosoma* finds conditions for existence at an optimum and the introduction of this fish into such waters is to be avoided if a high level of game-fish production is desired. Wiebe (*in* Hubbs 1934: 60-61) noted that stocking gizzard shad in ponds at Burlington, Iowa, resulted in overpopulation of the species.

In many other waters the gizzard shad is a highly esteemed forage fish. Wickliff (1933: 275) stated, "Upon the presence or absence of this fish seems to rest the burden of whether or not impounded waters in Ohio will be productive of several game fish * * *." This author pointed out that *D. cepedianum* does not compete appreciably with other fishes in spawning sites or in general habitat preference, that it cannot be depleted by angling, and that it makes an attractive bait. Its chief drawbacks are a natural mortality in the spring and fall and sensitivity to handling. In the deep, clear reservoirs of the Tennessee River system, young-of-the-year gizzard shad constitute the most important food source of the game species taken from deep as well as from shallow water. Continuous cropping of this year class leaves just a sufficient nucleus of adults to maintain a large number of young, so that the forage fish-predator relation is in nearly perfect balance.

In experimental combinations of gizzard shad with bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) in Alabama ponds, Swingle (1949: 53-55) showed that although a relatively high poundage of largemouth bass resulted from a shad-bass combination, the yield was not sufficient to justify omission of bluegills and, when that species was added, large

shad accumulated and reduced the size of the adult bluegills with which they competed for food.

In discussing the management of Indiana ponds for fishing, Krumholz (1952: 256) wrote that gizzard shad should not be stocked in the ponds of that State, but gave no reasons.

The gizzard shad is said to be by far the most abundant species in the larger impoundments of Oklahoma and to assure an ample food supply for game fishes throughout the summer months (Jenkins 1951: 93). The species is fast-growing and rather short-lived, and, although its rapid growth eliminates the gizzard shad from a size range suitable for food of the smaller game fishes, the large crop produced each year offsets this disadvantage (Jenkins 1953b: 36).

After a study of 22 warm-water artificial lakes in Illinois, Bennett (1943: 364) wrote:

Gizzard shad were present in 10 of the 22 lakes. In some cases they were introduced by floods from nearby streams. In others they were stocked as forage fish. They are not satisfactory for this purpose in artificial lakes because they reproduce in tremendous numbers and rapidly become too large to be eaten by the game fish present. In almost every case, large shad populations were associated with small numbers of bass. In 5 of the 10 lakes the shad constituted from 48 to 65 percent of the entire fish populations (by weight) and the game and pan fish were small and stunted.

Dorosoma cepedianum is a valuable forage fish but under certain conditions it is not suitable for this purpose. In shallow, warm-water lakes with mud bottom, high turbidity, and high fertility, it is likely to get out of control, even if numbers of predatory game fishes are present. This is particularly true if the species is not native to such waters. It is ideal for forage use in fluctuating impoundments (such as Norris Reservoir, Tenn.) where the water is deep and clear, the shoreline is abrupt, no littoral vegetation develops, there is a paucity of benthic flora and fauna but adequate plankton, and sufficient predatory species are present to crop the young-of-the-year. It is also valuable in many waters that are somewhat intermediate between these two extremes, particularly where it forms a part of the native fish fauna which also includes a number of predatory fishes.

Range.—A detailed discussion of the northern limit of the gizzard shad was published recently (Miller 1957: 105-108). However the species may

have entered the Great Lakes, it is known today from Lake Erie, the southern parts of Lake Huron and Lake Michigan (which it has very recently invaded), and the Lake Ontario basin (Greeley 1940: 68). Specimens were taken recently in the St. Lawrence River near Quebec (Vladykov 1945). The erroneous records of this species from New Brunswick have been further discussed by Scott and Crossman (1959: 30).

The species ranges from southeastern South Dakota and central Minnesota, the Great Lakes drainage, and extreme southern New York, southward through the Mississippi River system and along the Atlantic slope to the Gulf coast of the United States and to the basin of the Río Pánuco in eastern México.

That the species has also entered the artificial canals and thus extended its range seems well founded. It has entered Lake Michigan by moving through the Chicago River Canal, and its occurrence at the northern end of Cayuga Lake, N.Y., has been plausibly credited to its transport there from Lake Erie by way of the Erie Canal. Wright (1918: 544) wrote, "The most recent Erie contribution in the mouths of our Ithaca streams is the gizzard shad (*Dorosoma cepedianum*) * * *." Greeley (1928: 95) recorded about 20 specimens taken November 11, 1916, from Cayuga Lake (evidently the same fish referred to by Wright), with the notation that fish presumably of this species were reported to have come through the Erie Canal one winter, many dying under the ice.

SUMMARY

Because of its importance to fishery workers, the gizzard shad, *Dorosoma cepedianum*, is treated in detail. Series of specimens from throughout its wide range form the basis for a summary of taxonomic characters and variation; no subspecies are recognized.

Dorosoma cepedianum spawns near the surface in fresh water from about the middle of March to the latter part of August, over a water temperature range of about 50° to 70° F. The eggs are sticky and demersal and, at times, may cover aquatic plants. The fertilized egg is nearly transparent and measures about 0.75 mm. in diameter after fixation. The embryology and early life history are described and figured.

The gizzard shad usually matures in its second or third year and may live to be 10 years old, but it typically does not attain an age greater than 5 to 7 years. In the northern part of its range, it may mature at about 6 inches in total length. From 70 to 80 percent of its annual growth occurs during June–August or July–September, depending on the season and the age of the fish. Fish 10 to 13 inches long weigh about 1 pound. The species commonly attains total lengths between 10 and 14 inches; the largest known individual was 20.5 inches long and weighed 3 pounds 7 ounces. No sexual dimorphism has been demonstrated for growth rate or in the length-weight relation. There are no reliable external characters by which the sexes may be distinguished.

Except for a few weeks after hatching, *D. cepedianum* is almost entirely herbivorous, feeding heavily on microscopic plants, phytoplankton, and algae. Once the early zooplankton stage is passed the diet is remarkably alike at various sizes. The species is essentially a filter feeder.

At least 17 important game fishes may eat gizzard shad, usually the young-of-the-year about 2 to 5 inches long; walleyes, however, may utilize individuals 8 inches or longer. Its importance as a forage fish is emphasized by the short food chain (direct utilization of phytoplankton), high reproductive capacity and abundance, general freedom from parasites, and rapid growth rate. At times, however, the species so overpopulates some waters that expensive means of control are necessary. Gizzard shad may become a nuisance in warm, shallow lakes that have a soft mud bottom, high turbidity, and relatively few predators; this is particularly true if the species is not native to such waters. In many other waters the gizzard shad is a highly esteemed forage fish, and it is particularly valuable for this purpose in fluctuating impoundments which have deep and clear water, an abrupt shoreline, little or no littoral vegetation, adequate plankton (but a sparse benthic flora and fauna), and sufficient predatory fishes to crop the young-of-the-year.

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DEVELOPMENT OF EGGS AND LARVAE OF
PACIFIC MACKEREL AND DISTRIBUTION
AND ABUNDANCE OF LARVAE
1952-56

BY DAVID KRAMER
Drawings by George M. Mattson



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ABSTRACT

This is a study of the eggs and larvae of the Pacific mackerel, *Pneumatophorus diego* (Ayres), a scombrid fish occurring off the west coast of North America from southeastern Alaska to central Mexico. The gross development of the eggs and larvae (including morphometry and ossification) are described, and data are given for the distribution and abundance of larvae from 1952 through 1956.

Embryonic development is described from the blastodisc stage until just before hatching. The yolk-sac larva and characteristic pigmentation changes in early and late stage larvae are described.

Straight line regressions for growth were found for the following characters in relation to standard length: head length, body depth, and distances from snout to anus and snout to first and second dorsal fins.

The order of ossification is given for some head bones, and for the spines and rays in the fins as follows: caudal, pectorals, second dorsal and anal, first dorsal, dorsal and anal finlets, and ventrals. Ossification of the vertebral column and its parts are described, including the centra, urostyle, hypurals and epurals, vertebral arches and spines, ribs, epipleurals, zygapophyses, and parapophyses. Development of the fin and finlet interspinal systems are described with particular emphasis on the individual parts of the interspinal processes, especially those forming the dorsal slot of the first dorsal fin. The development and appearance of the caudal keels is discussed in some detail.

Distribution of Pacific mackerel larvae is discussed for the years 1952 through 1956; census estimates of abundance are given by area and month. Vertical distributions of eggs and larvae are based on three night series which contained larvae; only one of which contained eggs. Areal distribution in relation to temperature was determined at the 10-meter level for all net tows containing Pacific mackerel larvae.

DEVELOPMENT OF EGGS AND LARVAE OF PACIFIC MACKEREL AND DISTRIBUTION AND ABUNDANCE OF LARVAE 1952-56

By DAVID KRAMER, *Fishery Research Biologist*, BUREAU OF COMMERCIAL FISHERIES

This is a study of the eggs and larvae of the Pacific mackerel, *Pneumatophorus diego* (Ayres), a scombrid fish occurring off the west coast of North America from southeastern Alaska to central Mexico. Specifically, the gross development of the eggs and larvae (including morphometry and ossification) are described, and data are given for the distribution and abundance of larvae from 1952 through 1956. This study is a part of a broad investigation of the population dynamics of the Pacific sardine (*Sardinops caerulea*) with which the Pacific mackerel is ecologically and economically associated. Other ecological associates of the sardine which have been subjects of similar studies include the jack mackerel, *Trachurus symmetricus* (Ahlstrom and Ball, 1954), and the hake, *Merluccius productus* (Ahlstrom and Counts, 1955).

These investigations are part of the California Cooperative Oceanic Fisheries Investigations sponsored by the California Marine Research Committee, and carried on through the cooperation of the Scripps Institution of Oceanography of the University of California, the California Department of Fish and Game, the California Academy of Sciences, the Hopkins Marine Station of Stanford University, and the South Pacific Fishery Investigations of the United States Bureau of Commercial Fisheries.

Until 1936, the Pacific mackerel was the third largest fishery in southern California, surpassed in tonnage only by those of the Pacific sardine and tuna. In a period of 18 years, from the seasons 1935-36 to 1953-54, the Pacific mackerel catch gradually declined from a peak of 73,000 tons to a low of 3,800 tons. This decline, although not unnoticed, was somewhat obscured by the more spectacular loss of the sardine fishery to the industry during these years (Fitch, 1952).

NOTE.—Approved for publication July 21, 1959. *Fishery Bulletin* 174.

In the 1954-55 season the Pacific mackerel catch increased to about 13,000 tons, which may have been due in part to an increase in temperatures along the southern California coast and to an influx of the mackerel from southern waters.

Unlike the sardine, anchovy, hake, and jack mackerel, the Pacific mackerel is not one of the more abundantly spawned pelagic fishes in the area being investigated. Its spawning is sporadic and generally distributed in the same areas as that of the Pacific sardine (figs. 17-21, and Ahlstrom 1954a). The chief spawning areas on the west coast are in Sebastian Vizcaino Bay near Cedros Island, and south of Point Eugenia to Cape San Lucas, Baja, Calif. It has been demonstrated by movements of tagged fish that the Pacific mackerel is migratory, moving north and south with the changes in season (Fry and Roedel, 1949; Roedel 1949b). Thus, it is reasonable to assume that cold waters in the former northern range (the fishery once having extended to British Columbia) have kept the migratory pattern limited to the northernmost extent of the warm southern waters. The low catches and the low larval populations from 1949 through 1953 may have resulted in part from an extension of these cold waters to southern California. This may be partly corroborated by the following facts: (1) the commercial catch in southern California in the 1954-55 season exceeded that of the 1953-54 season by 340 percent, and (2) the larval population in 1954 exceeded that of 1953 by more than 90 percent.

It is with sincere pleasure that I acknowledge the collection of the data and material for this study by the employees of the Scripps Institution of Oceanography and the California Department of Fish and Game, and its preparation by the staff of the South Pacific Fishery Investigations. I am particularly indebted to E. H. Ahlstrom for his invaluable criticism and guidance in the prep-

aration of this paper, and to John C. Marr, Bruce Taft, and Charles P. O'Connell for review of the final manuscript. I wish also to thank James R. Thraillkill for the preparation of the annual distribution charts, Andrew M. Vrooman for the preparation of the graphs, and George M. Mattson for the illustrations and for assistance in diagnosing many of the structures described here.

OTHER STUDIES OF MACKEREL

The only previous investigations of the egg and larval development of the Pacific mackerel are those by Fry (1936a), Roedel (1949a), and Orton (1953). Fry's work was based on living material and illustrated with drawings of four stages of embryonic and three stages of larval development. Orton's study of the development and migration of pigment cells in teleost fishes included the Pacific mackerel, illustrated with drawings, from live material, of two embryonic stages and three larval stages through 2 days old. Roedel's paper dealing with spawning grounds and life history of the Pacific mackerel was illustrated with five drawings of the external anatomy of the larvae and three stages of the sequence of ossification.

Although there have been many investigations of the distribution and fisheries of the Japanese mackerel, *Pneumatophorus japonicus* (Houttuyn), few are concerned with the development and life history. Kamiya's descriptions and illustrations of the eggs and larvae of the Japanese mackerel (1925) are similar to those of the Pacific mackerel. Kishinouye (1923) provided an estimate of the ages of the juveniles from 12 to 35 centimeters in length, and illustrated a 40-millimeter juvenile.

There are no descriptions of the egg and larval development of any of the other species of *Pneumatophorus*.

The fisheries for the Atlantic mackerel, *Scomber scombrus* Linnaeus, are among the oldest and more important in the world, and the life history of this fish has been the subject of numerous investigations, the most complete of which are the studies by Sette (1943 and 1950). No single, complete study has been made but there are many publications describing the egg of this mackerel and various stages of its larval development (Cunningham 1891a and b; Sette 1943). Fry (1936a) stated that the similarity of the Pacific mackerel

egg to that of the Atlantic mackerel facilitated the identification of the former.

Genus *PNEUMATOPHORUS*

Species and Distribution

The mackerels of the genus *Pneumatophorus* Jordan and Gilbert are those with air bladders. The generic name is derived from the Greek words *pneumatōs*, meaning air, and *pheros*, meaning to bear or carry. Literally translated, the genus may be designated as "air bearing," or that which carries air. Starks (1921) elevated the subgenus, *Pneumatophorus* of the genus *Scomber* Linnaeus, to full generic status on the basis of the presence of an air bladder. No attempt will be made here to differentiate the species of *Pneumatophorus* beyond noting their distributions. Detailed studies of meristic characters and body proportions were made by Jordan and Hubbs (1925) on all species; by Fitch¹ on *P. diego*, *P. peruanus*, and *P. australasicus*; and by Murakami and Hayano (1956), and Abe and Takashima (1958) on *P. japonicus* and *P. tapeinocephalus*. The broader groupings and classifications followed in this paper are those of Shultz (1948) and Fraser-Brunner (1950) who place the mackerels and tunas in the family Scombridae.

There is still discussion among ichthyologists concerning the rank of *Pneumatophorus diego* (Ayres). Some consider *P. diego* to be a subspecies of the Japanese mackerel, *P. japonicus*. In accordance with general usage (Amer. Fish. Soc., 1948; Roedel, 1953), I consider the local form to be a distinct species, *P. diego*.

The world-wide distribution of the genus *Pneumatophorus* is as follows:

P. diego (Ayres): Northeast Pacific ocean; all of the Gulf of California; southward to Bandaras Bay, Mexico (Fitch²): at one time to northwest Alaska (Rounsefell and Dahlgren, 1934), now possibly only as far north as Point Conception, as determined from larval populations.

P. peruanus Jordan and Hubbs: Southeast Pacific ocean, Santa Elena Bay, Guayaquil, Ecuador, to the coasts of Peru and Chile; common at Panama at certain times (Fitch²); known also from the Galapagos Islands.

P. colias (Gmelin): Temperate Atlantic ocean: north to outer Nova Scotia and the Gulf of St. Lawrence in the west, to England in the east.

P. japonicus (Houttuyn): Indefinite range in the

¹ John E. Fitch, California Department of Fish and Game. Mr. Fitch kindly loaned me his notes and tabulations, which show a definite revision of the earlier work by Jordan and Hubbs on these three species.

² By correspondence.

Pacific ocean; Japan, south to the Philippine Islands, Australia, Indian Ocean, and South Africa.

P. australasicus (Cuvier and Valenciennes): North coast of Australia from Moreton Bay, Queensland to Lord Howe Island; Hawaii and Socorro Island off the west coast of Mexico; Revilla Gígedo Islands (Fitch).

P. tapeinocephalus (Bleeker): Japan, coastwise, near shore.

P. grex (Mitchill): Western north Atlantic ocean, east coast of North America.

Some attempts have been made to differentiate regional races of the Pacific mackerel on the Pacific coast. These have been based on differences in abundance in defined areas, and differences in meristic characters (Roedel 1952; Royce 1957). The specimens examined for this paper were taken from the complete range of the cruises of the California Cooperative Oceanic Fisheries Investigations, including many samples from the Gulf of California. If separate races exist, they could not be distinguished in the larvae or young juveniles by any of the methods used and described in such investigations.

DEVELOPMENT OF THE EGG

The development of the Pacific mackerel egg is similar to that of most pelagic fish eggs. Detailed reports have been published on the development of the eggs and larvae of the jack mackerel (Ahlstrom and Ball, 1954) and the hake (Ahlstrom and Counts, 1955). The eggs of these fishes are similar in size and appearance to those of the Pacific mackerel. However, careful study and comparison of the three reveals that there are many easily discernible differences. It is seldom that the eggs of all of these fishes are found at the same time. When found together, they are usually in some combination of two. Batches of eggs having many early stages of any one of these three species usually have several later stages of development present, which can be identified easily. It

can be assumed then that the early stages of eggs of the same diameter, same size oil globule, and the same type of yolk are of the same species. Another aid (not used here) in the identification of mixed species is the method devised by Sette (1943) to separate Atlantic mackerel eggs from those of other species. He made scatter diagrams of oil-globule diameter plotted against egg diameter and found that when mackerel eggs were near the extremes of the size limits of their overall range, and could be expected to overlap the ranges of other fish species, the eggs of the other fishes were also near the corresponding limits of their size ranges, and the groups remained discrete.

The Pacific mackerel egg is spherical, with an average diameter ranging from 1.06 to 1.14 mm. (table 1). The yolk is clear and at magnification (36x) can be seen filled with many tiny vacuoles. Staining showed that these vacuoles do not contain oil; no further study was made of them. There is a single oil globule with an average diameter of 0.26 mm. The yolk size and the width of the perivitelline space in preserved specimens are not typical of the living egg, owing to the shrinkage and distortion of the yolk mass. Since preserved eggs were used for the illustrations in figures 1 and 2, the yolk masses were idealized to approach more closely Fry's description (1936a and table 2) of the perivitelline space.

Fry's study (1936a) of Pacific mackerel eggs from southern California led him to conclude that the eggs found at the beginning of the spawning season were larger than those found at the end of the season. Similar observations were made by Sette (1943) in the study of the Atlantic mackerel, and by Ehrenbaum (1921) on the European mackerel. Pacific mackerel egg and oil globule diameters as reported by Fry (1936a) and as determined from my material are given in table 1.

TABLE 1.—Comparison of egg size in Pacific mackerel

Collection	Location	Time	Egg diameter			Oil globule		
			Number of specimens	Range (mm.)	Average (mm.)	Number of specimens	Range (mm.)	Average (mm.)
Fry ¹	Southern California	May	(²)	to 1.35	1.2	(²)		
Fry	do	June-July	(²)	0.9-1.2	1.05-1.08	(²)	0.26	
CCOFI ³	Gulf of California	Feb. 1956	244	0.98-1.17	1.11	151	0.24-0.31	0.26
Do	do	Apr. 1956	264	0.80-1.17	1.06	264	0.22-0.31	0.26
Do	Southern California	May 1956	50	1.07-1.20	1.14	50	0.24-0.29	0.27

¹ Fry (1936a).

² Number of specimens examined was not indicated by author.

³ California Cooperative Oceanic Fisheries Investigations.

TABLE 2.—Characters used to distinguish eggs and newly-hatched larvae of the Pacific mackerel, jack mackerel, and hake

Item	Pacific mackerel	Jack mackerel ¹	Hake ¹
EGG			
Size.....	1.06 to 1.14 mm.....	0.96 to 1.02 mm.....	1.07 to 1.18 mm.....
Oil globule.....	0.26 to 0.27 mm. Off center from polar axis.....	Single—0.25 mm. On center on polar axis.....	Single—0.30 mm. Off center from polar axis.....
Yolk.....	Clear—magnification shows tiny vacuoles throughout yolk mass. ²	Segmented.....	Clear.
Perivitelline space.....	Narrower than either hake or jack mackerel—about 0.02 mm. wide. ³	Moderate (0.09 mm. wide).....	Moderate (0.06 mm. wide).
Pigmentation:			
Yolk.....	On yolk near pectoral region.....	None.....	On yolk near head.
Embryo.....	Dorsal pigment first one line head to tail; splits laterally to two dorsal lines when tail grows away from yolk; before hatching head becomes fairly heavily pigmented and body pigment begins ventral migration.	Dorsal pigment extends most of length of embryo; ventral pigment occurs behind anus; pigment seldom occurs forward of the eyes.	Dorsal pigmentation continuous in middle-stage eggs; separates into patches in later-stage eggs.
Number of myomeres.....	31.....	24.....	51 to 54.
YOLK-SAC LARVAE			
Size.....	3.0 to 3.5 mm.....	2.07 mm.....	2.4 mm.
Pigmentation.....	Some dorsal pigment; most pigment migrating ventrally.	Dorsal and ventral retained.....	Collects in patches.
Oil globule.....	In rear of yolk-sac.....	Under head in forward portion of yolk-sac.	In rear of yolk-sac.

¹ Ahlstrom and Counts (1955). ² The same noted in hake eggs. ³ Fry (1936a).

Using the method of description of Ahlstrom and Ball (1954) and Ahlstrom and Counts (1955), the following study of the development of the Pacific mackerel egg is divided into three stages: early (fertilization through closure of the blastopore), middle (blastopore closure to the twisting of the tail from the embryonic axis), and late (tail twisting to hatching). Table 2, taken in part from Ahlstrom and Counts (1955), was prepared to show the differences in the eggs and yolk-sac larvae of the jack mackerel, hake, and Pacific mackerel.

EARLY-STAGE EGGS

In the early stage, the distinguishing characters of the Pacific mackerel egg are egg size, oil globule size, and clear yolk with many small vacuoles (distinguished at 36x magnification) scattered throughout the yolk mass. Egg size and oil globule size differentiate Pacific mackerel from hake eggs. Smaller size and segmented yolk distinguish jack mackerel eggs from the two. Between the time of the formation of the blastodisc and the closure of the blastopore in Pacific mackerel (fig. 1a-c; also in hake eggs) the oil globule at the vegetative pole is not centered on the polar axis, but is located offcenter. Thus, it appears close to the tail area at the time of blastopore closure, and close to the anus as the tail grows around to the head. On hatching, it is located in the posterior portion of the yolk sac. In the jack mackerel, the oil globule remains almost centered on the polar

axis between the head and the area where the tail grows away from the yolk mass. Therefore, it is located under the head in the anterior part of the yolk sac at hatching.

MIDDLE-STAGE EGGS

At about the time of blastopore closure the eyes become differentiated (fig. 1c). Very soon after the blastopore closes, pigment appears on the dorsum of the embryo from the area just posterior to the eyes, extending almost to the end of the tail. This pigmentation extends laterally to the yolk mass in many places along the sides of the embryo. At this time, too, the head begins to widen laterally. The head tends to form a triangle, with the widest section posterior to the eyes and the narrowest part just posterior to the pectoral region. The body width at the pectoral region is three-fourths the head width. By the time the tail bud forms, the head has grown to a width that is about twice that of the body at the pectoral region. This approximate ratio is maintained until hatching. Between the time the tail bud forms and the tail twists out of the body axis, the pigment on the back divides to form a V with the open end posterior to the eyes and the closed end on the dorsum behind the pectoral region (fig. 1d). Posterior to this point, the pigment divides again to form two lines on either side of the midline, extending almost to the tip of the tail. Because of the slight depth of the body, some of the

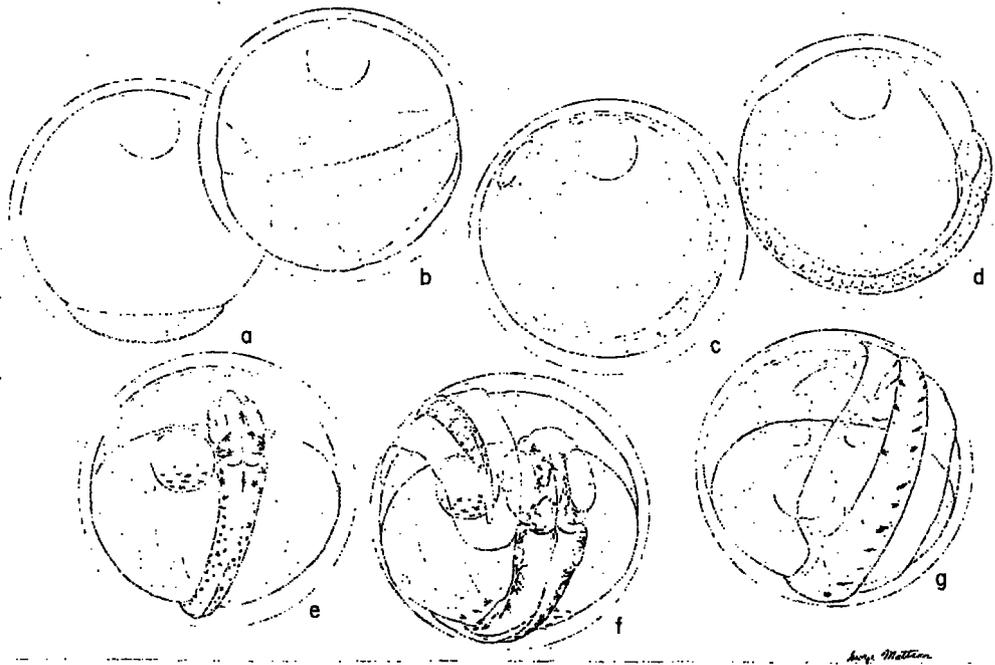


FIGURE 1.—Development of the egg of the Pacific mackerel, *Pneumatophorus diego*: a, b, and c, early embryonic development, c being the early stage immediately before blastopore closure; d, middle-stage, just after blastopore closure; e, middle-stage, dorsal view of head and pectoral region, tail separated from yolk sac; f, late-stage, tail reaching to head; g, same as f, viewed from opposite pole.

pigment forming these two lines extends laterally as far as the yolk sac.

LATE-STAGE EGGS

As the tail begins to twist out of the embryonic axis, the body becomes deeper and the pigment on its sides begins to coalesce into a definite pattern of two, lightly scattered lines, the pigment near the tail being more or less patchy. The pigment seems to be migrating at this time, but it is only stretching-out along the sides with the deepening of the body. The heaviest concentration of pigment is in that area forming the V between the eyes and the pectoral region. A line of pigment sometimes connects the open ends of the V across the area just behind the eyes. A heavy line or fold to the oil globule can now be defined from the point at which the tail leaves the yolk mass. This line develops into the posterior section of the intestine ending in the anus. The caudal fin fold becomes differentiated at this time. When the tail is about halfway to the head, pigment appears on the head slightly forward of the eyes and on the sides of the head behind the eyes. Pigment is

now lightly scattered on the oil globule on the hemisphere oriented toward the head.

By the time the tail extends as far forward as the head, the pigment is migrating ventrally on the sides of the body. In most specimens, more pigment appears on top of the head. Most of the pigment on the sides of the body is still concentrated behind the pectoral region about one-third the body-length posterior to the head (fig. 1f). At about this time, pigment can be seen to be migrating from the sides of the body onto the yolk sac, and as development proceeds it spreads out and forward over the yolk to the areas on the yolk sac near the head.

Just before hatching (fig. 2a) the tail extends forward of the head. The head is heavily covered with pigment to the snout. All the pigment on the sides of the body is migrating ventrally. There is a single, ventral line of pigment near the tail and some still dorsolateral on both sides above it. The oil globule is three-fourths covered with pigment. The anus and intestine are well formed behind the oil globule.

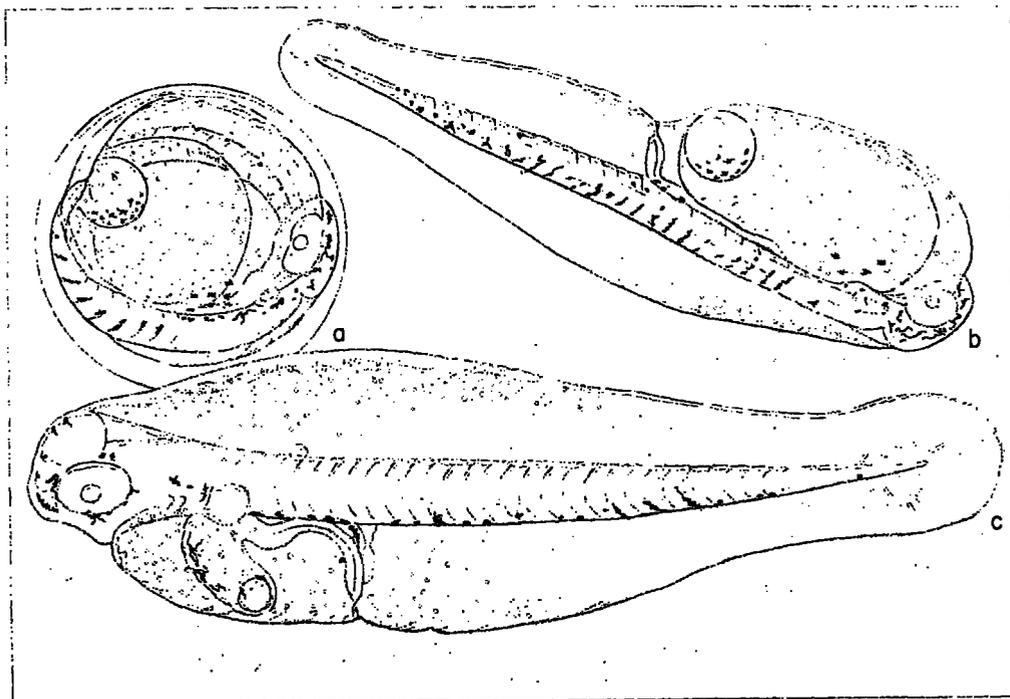


FIGURE 2.—Late-stage egg and yoke-sac larvae of the Pacific mackerel, *Pneumatophorus diego*: a, egg immediately before hatching; b, yoke-sac larva, 3.3 mm. long, just after hatching; c, yoke-sac larva, 3.5 mm. long, with yoke about two-thirds absorbed.

DEVELOPMENT OF THE LARVAE THROUGH THE JUVENILE STAGE

VARIATIONS IN DEVELOPMENT

The Pacific mackerel larvae used in this study were grouped by 0.5-mm. intervals for specimens between 2.50 and 10.99 mm. in length, and by 1.0-mm. intervals for specimens longer than 11.0 mm. Rates of development of individual larvae may not differ very much from the average in certain characters, yet differ considerably in others. A fairly consistent sequence of development with increase in larval length is usually found in pigment changes and in changes in body proportions. These usually take place within length differences of one-half millimeter. The sequence in which ossification of structures takes place is usually constant (fig. 9). However, the time of development of some structures may show considerable variation. One extreme example, was the limited ossification of an 8.67 mm. larva. Larvae of this size usually had the vertebral column at least as well developed as the specimen shown in figure 15e, but this larva was no more developed than

that of a 6.0 mm. larva (fig. 15a) and the rays had not yet developed in the pectoral, dorsal, or anal fins. On the other hand, ossification of teeth, caudal fin, branchiostegals and gill rakers were as well developed on this specimen as on other larvae in its size group.

The larval characteristics recorded, described and illustrated in this paper are average ones, and presented as such, and these differences must be kept in mind when the various stages are discussed and finite figures are used as illustrations.

Considerable development of the Pacific mackerel larva takes place between the time of hatching and the completion of yolk absorption, including mouth formation, pigmentation of the eyes, and development of pectoral fins (with rays). According to Fry (1936a) yolk absorption requires about 2½ to 3 days, after which the larva is developed enough to forage for itself.

PIGMENTATION CHANGES

The pigmentation of the yolk-sac larva of the Pacific mackerel is very much like that described for the embryo just previous to hatching. It is

characterized chiefly by the ventrally migrating pigment on the sides of the body. Characteristic pigmentation of early larval stages after yolk absorption includes a few pigment spots on top of the head, and a double line of ventral pigment extending from the anus almost to the tip of the tail. The pigmentation of later-stage larvae consists primarily of melanophores on top of the head, pigment on the posterior two-thirds of the dorsal surface, a vertical line or patch of pigment at the base of the tail, dashes of pigment along the lateral line in posterior portions of the body, and a line of pigment from the anus to the caudal peduncle. Juvenile pigmentation is heaviest on the back, top of the head, and in the peritoneal cavity, the greatest concentrations being on the dorsal surface of the body and on the head in which clear sections occur only on the operculum, the area around each nostril, and the surfaces ventral to the mandibles.

Pigmentation: yoke-sac stage

The newly-hatched Pacific mackerel larva, which is about 3.0 mm. in length (fig. 2*b*), has no definite pattern of pigment. Pigment on the head is often rather heavy, extending from the region over the brain forward to and under the snout. The pigment on the body is migrating ventrally with some of it already on the ventral surfaces. Pigmentation on the yolk sac is light and, having originated from the body, is generally restricted to the dorsolateral surfaces. The oil globule is heavily pigmented on its anterior hemisphere with some pigment scattered on its posterior sections.

When the yolk sac is about one-fourth absorbed, the preserved larva looks very much like the 8-hour larva drawn and described by Fry (1936*a*; fig. 12*f*). There is very little change in pigment except that some has migrated onto the intestine at that place where it is detached from the body above the anus. The length of the body is about the same as at hatching.

At about 3.5 mm. (fig. 2*c*) the yolk sac is almost two-thirds absorbed. The shape of the head is dome-like above the eyes and slants forward to the snout which extends forward to project over the lower section of the head. The anteroventral rim of the eye extends almost to the ventral edge of this projection. The pigment on the head forms

a ring over each eye and on the forward part of the head from the dome to the snout. Pigment sometimes extends laterally and posteriorly in lines along the junction of the eyes and head. These lines sometimes extend and meet the pigment in the horizontal lines in back of the eyes on the lateral surface of the head and body just above the yolk sac. Except for a few scattered melanophores on the body, the pigment has migrated completely to the ventral surfaces of the body. A heavy concentration of pigment can be seen on top of the body cavity extending almost to the anus. Posterior to the anus, the ventral pigment on the body is in two lines, one on each side of the ventral fin fold. There is a heavy concentration of pigment on the ventral surface of what remains of the yolk sac. This is probably due to the fact that most of the pigment on the yolk-sac surface has been pulled together as the yolk is absorbed.

Pigmentation: larval period

When the yolk is completely absorbed, all the pigment disappears from the head except about 3 to 5 melanophores on the occipital region. This condition persists until the larva is about 5.0 mm. in length (fig. 3 *a* and *b*). These melanophores increase in number and size, each of them becoming rather large and distinctly circular. They retain their shape and position throughout the larval and early juvenile stages.

At about 7.0 mm., pigment appears forward of the occipital region, and very shortly thereafter on the snout. These pigment areas increase rapidly in size until, at about 7.5 mm., the top of the head is usually covered from snout to nape. Also, at this time melanophores begin to appear on the mandible and operculum. Pigmentation increases both on the top and sides of the head until the head is completely covered, but there is no pigment on the underside of the head (fig. 4).

In late yolk-sac larvae there is sometimes a small patch of dorsal pigment at about the twenty-third myomere. This is sometimes seen in specimens that have been preserved for a great length of time, but more often in freshly preserved material. Fry's illustration of this stage (1936*a*; fig. 12 *g*) shows this patch on a live specimen.

After yolk absorption, two or three characteristic pigment spots appear on the ventral surface of the gut and are retained there (fig. 3 *a-d*) until

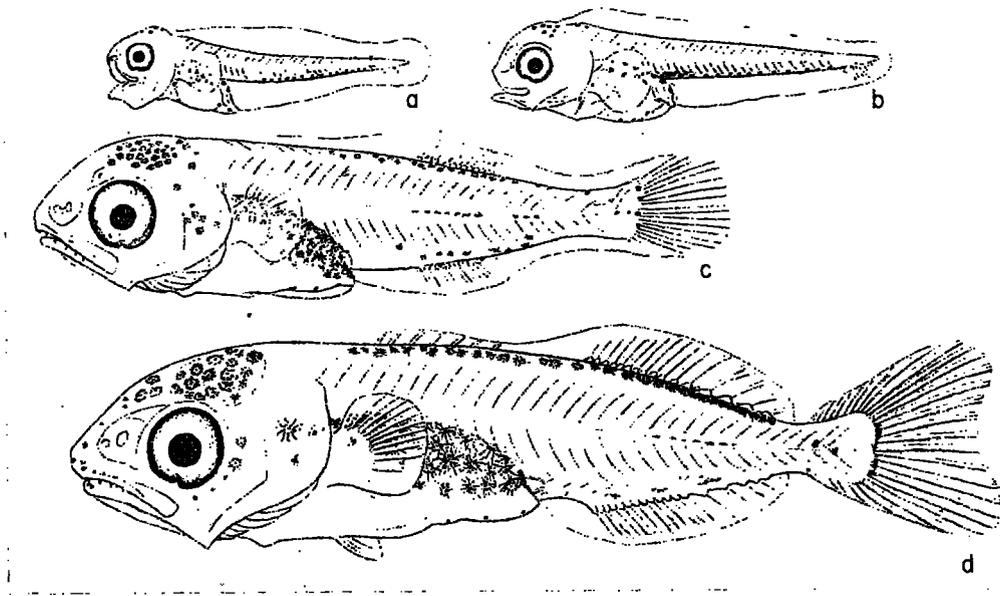


FIGURE 3.—Development of the larva of the Pacific mackerel, *Pneumatophorus diego*: a, larva 4.0 mm. long; b, larva 5.0 mm. long; c, larva 7.8 mm. long; d, larva 10.5 mm. long.

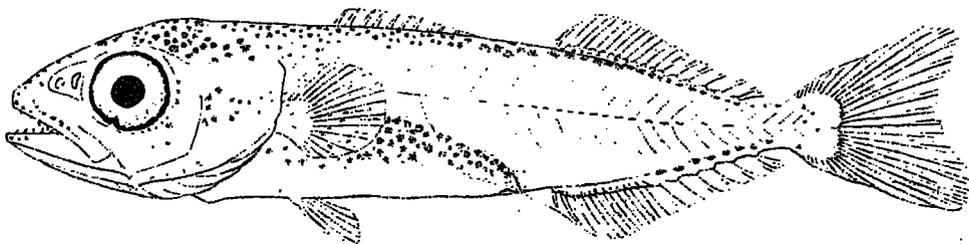


FIGURE 4.—Late larva of the Pacific mackerel, *Pneumatophorus diego*, 16.5 mm. long.

they are absorbed or disappear in the late stages.

The pigment in the region of the developing caudal fin becomes apparent at about 5.0 mm. It is scattered and has no particular pattern. In the area adjacent to the last myomeres, a small patch appears and is retained through further growth (fig. 3*b*). At about 6.0 mm., the posterior tip of the notochord has turned dorsally and pigment spots form a vertical line at the base of the caudal fin (fig. 3*c*).

When the larva is about 7.0 mm. in length, the first well-defined dorsal pigment appears at about

the sixteenth myomere. Dorsal pigment spreads rapidly, and at about 8.0 mm. a double line of melanophores forms between the sixteenth and twenty-seventh myomeres. Simultaneously, a second group of melanophores appears at approximately the seventh and eighth myomeres, and increases rapidly to meet the posterior group at a point above the origin of the anal fin. The posterior dorsal pigment is always much better defined than the anterior group during the larval period (fig. 3*c* and *d*).

At about 7.4 mm., lateral line pigment appears

(fig. 3c). Ahlstrom and Ball (1954) describe this as the post-anal, lateral line streak in the jack mackerel, and refer to its presence in the larvae of several other species of carangid fishes. At this size, the double row of ventral pigment posterior to the anus becomes single, and can be seen inside the dermal layer.

Pigment in the gut region is confined to the peritoneal cavity until the larva is about 7.5 mm. in length. At this time a few melanophores appear on the sides of the gut and then gradually increase in numbers until its lateral areas are covered with pigment. The peritoneal cavity becomes opaque at about 9.0 mm., but the dark pigmentation can still be defined in it even in individuals up to 15.0 mm. in length.

When the larva hatches, the eyes have no pigment. The first pigment appears on the iris in a semicircle ventral to the lens, when the yolk sac is about one-third absorbed. There may also be a small patch of pigment on the anterior-ventral surface of the iris. When the yolk sac is almost absorbed there is a complete circle of pigment on the iris around the lens. Then most of the pigment begins to form on the dorsal and dorsolateral surfaces. The final process of pigmentation is circular around the outer rim of the eye, the last part to become solidly pigmented being the highest sections on the ventrolateral and dorsolateral surfaces of the iris.

CHANGES IN BODY FORM

All specimens of the Pacific mackerel studied for changes in body form and sequence of ossification were cleared and stained by a process modified after the one described by Hollister (1934). Measurements and meristic counts were made on cleared and stained material. Measurements are made more easily on specimens prepared in this manner because reference points on the skeleton or on the body outline in relation to skeletal structures can be established and kept constant.

In its early larval stages in the sizes measured after yolk absorption, the Pacific mackerel is deep-bodied and stubby. As it approaches the juvenile stage it begins to assume the fusiform shape which is typical of all adult scombrids. The juvenile stage of the Pacific mackerel can be said to begin after all the fins have ossified all or part of their

spines and rays. This takes place between 18.9 and 24.6 mm. Unlike the hake, but more like the jack mackerel, the distance from the snout to the anus in the Pacific mackerel is approximately two-thirds of the body length.

The data for all measurements and meristic³ counts are summarized in tables 3 and 4. The measurements in columns are averages for the numbers of specimens listed for each size group. The meristic counts are given as ranges rather than averages because of the variations in the development of individual fish within the same size group. These differences may result from intrinsic factors such as the slower or more rapid development of some individuals, or from extrinsic factors such as fading of stain from ossified parts. Some specimens, known to be sufficiently developed to show ossification up to a certain point, would stain so faintly or not at all that no

TABLE 3.—Measurements of Pacific mackerel larvae

Size group of standard length (mm.)	Number of specimens	Average morphometric measurements (mm.) ¹						
		Standard length	Head	Eye	Depth	Snout to anus	Snout to 1st dorsal	Snout to 2d dorsal
2.00-2.49	4	2.40	0.62	0.26				
2.50-2.99	21	2.78	0.65	0.31	² YS	1.17		
3.00-3.49	12	3.25	0.78	0.40	YS	1.19		
3.50-3.99	2	3.64	0.93	0.43	YS	1.50		
4.00-4.49	7	4.25	1.00	0.49		1.71		
4.50-4.99	17	4.72	1.20	0.57		1.96		
5.00-5.49	14	5.30	1.34	0.61		2.31		
5.50-5.99	29	5.74	1.51	0.68		2.59		
6.00-6.49	24	6.24	1.66	0.74		2.92		
6.50-6.99	23	6.70	1.78	0.79		3.25		
7.00-7.49	20	7.23	1.95	0.83		3.55		
7.50-7.99	5	7.76	2.09	0.87		3.90		
8.00-8.49	16	8.21	2.35	0.99		4.16		
8.50-8.99	5	8.79	2.49	1.06		4.71		
9.00-9.49	11	9.33	2.50	1.06		5.05		
9.50-9.99	2	0.72	2.80	1.09		5.28		
10.00-10.49	4	10.22	2.89	1.12		5.60		
10.50-10.99	2	10.68	3.10	1.18		6.34		
11.00-11.99	6	11.37	3.27	1.25		6.38		
12.00-12.99	1	12.70	3.75	1.48		7.02	4.32	7.36
13.00-13.99	5	13.50	3.92	1.42		7.90	4.80	8.25
14.00-14.99	4	14.49	4.19	1.40		8.48	5.10	8.77
15.00-15.99	4	15.48	4.45	1.50		9.18	5.57	9.56
16.00-16.99	5	16.55	4.78	1.58		9.80	5.85	10.20
17.00-17.99	3	17.20	4.95	1.64		10.54	6.28	10.77
18.00-18.99	1	18.90	5.50	1.71	4.00	10.92	6.42	11.14
						12.60	6.80	12.40

¹ See appendix for data on all specimens.

² Yolk-sac stage.

attempt was made to make or record meristic rates of ossification (see appendix). Table 5 gives the body proportions of Pacific mackerel larvae in percentages of standard length.

³ Although the term "meristic" is technically applied only to counts of the vertebral column and its associated structures, common usage has made the term applicable to all numerable body counts and it is used as such in this study.

TABLE 4.—Range of meristic counts in Pacific mackerel larvae¹

[One figure represents the fact that all specimens (one or more) in a size group had achieved only the number shown in that category. Where the number becomes constant in a column, the final count usually has been achieved.]

Size group of standard length (mm.)	Number of specimens	Vertebrae	Branchiostegal rays (left side)	Caudal		Pectorals		Second dorsal ²	Anal ²	Dorsal finlets	Anal finlets	First dorsal	Ventrals ²	
				Principal rays	Secondary rays		Left							Right
					Dorsal	Ventral								
2.00-2.49	4													
2.50-2.99	21													
3.00-3.49	12													
3.50-3.99	2													
4.00-4.49	7													
4.50-4.99	17													
5.00-5.49	14													
5.50-5.99	29													
6.00-6.49	24													
6.50-6.99	23	5-14	4-6	10-17										
7.00-7.49	20	4-16	5 or 6	10-17										
7.50-7.99	5	24	4-7	16-17	1 or 2	1 or 2	6 or 7	6 or 7	6	10				
8.00-8.49	16	20-31	6 or 7	17	1-3	1-3	5-8	5-9	7-11	7	1-4		IV	
8.50-8.99	5	25	7	17	2	1 or 2	7-9	7-9	8-I, 11	8-I, 11	1-4	1-4	VI	
9.00-9.49	11	23-31	7	17	2 or 3	2 or 3	5-10	6-10	7-I, 11	7-I, 11	1-3	1-3		
9.50-9.99	2	30	7	17	3	2 and 3	9	9	10 and 11	11	1	1		
10.00-10.49	4	30	7	17	3 or 4	3 or 4	9 or 10	8-10	I, 11	I, 11	2-5	2-5	IV	
10.50-10.99	2	31	7	17	2 and 4	2 and 4	10 and 11	10 and 11	I, 11	I, 11	5	5	IX	
11.00-11.99	6	31	7	17	3-6	3-6	10-14	10-14	11-I, 11	I, 11	5-6 ^{1/2}	5-6 ^{1/2}	VI-VIII	
12.00-12.99	1	31	7	17	7	7	15	15	I, 11	II, 11	6 ^{1/2}	6 ^{1/2}	X	
13.00-13.99	5	31	7	17	6 or 7	6-8	13-15	14 or 15	I, 11	II, 11	6 ^{1/2}	6 ^{1/2}	X	
14.00-14.99	4	31	7	17	6 or 7	6 or 7	15	14-16	I, 11	II, 11	6 ^{1/2}	6 ^{1/2}	X	
15.00-15.99	4	31	7	17	7 or 8	7 or 8	16 or 17	15-18	I, 11	II, 11	6 ^{1/2}	6 ^{1/2}	X	
16.00-16.99	5	31	7	17	7-9	7-9	16 or 17	15-18	I, 11	II, 11	5 or 6 ^{1/2}	6 ^{1/2}	IX or X	
17.00-17.99	3	31	7	17	9	9	16 or 17	17 or 18	I, 11	II, 11	6 ^{1/2}	6 ^{1/2}	X	
18.00-18.99	1	31	7	17	9	9	17	18	I, 11	II, 11	6 ^{1/2}	6 ^{1/2}	X	

¹ See appendix for data on all specimens.

² Second dorsal, anal, and ventral fins; arabic numeral alone represents early development; no differentiation between spines and rays. When roman numerals are used for spine counts, such spines are indicated on the basis of known adult counts, although actual differentiation may not be apparent.

³ Larval bud.

⁴ Larval pectoral.

TABLE 5.—Body proportions of Pacific mackerel larvae

Size group (mm)	Standard length (mm.)	Body proportions in percentages of standard length					
		Head	Eye	Depth	Snout to anus	Snout to 1st dorsal	Snout to 2d dorsal
2.00-2.49	2.40	25.83	10.84	¹ YS	48.82		
2.50-2.99	2.78	23.34	11.06	YS	43.03		
3.00-3.49	3.25	23.53	12.45	YS	46.08		
3.50-3.99	3.64	25.52	11.80	YS	46.94		
4.00-4.49	4.25	23.56	13.13		23.35	45.97	
4.50-4.99	4.72	25.46	12.10		24.70	49.05	
5.00-5.49	5.30	25.20	11.51		24.77	48.89	
5.50-5.99	5.74	26.38	11.80		25.46	50.79	
6.00-6.49	6.24	28.90	11.84		26.03	52.00	
6.50-6.99	6.70	28.59	11.81		25.59	53.00	
7.00-7.49	7.23	26.99	11.55		25.95	53.92	
7.50-7.99	7.76	26.95	11.15		25.16	53.56	
8.00-8.49	8.21	28.63	12.09		26.96	58.56	
8.50-8.99	8.73	28.27	12.10		26.28	57.44	
9.00-9.49	9.33	27.75	11.35		25.67	56.55	
9.50-9.99	9.72	28.74	11.21		25.76	57.58	
10.00-10.49	10.22	28.25	10.98		25.23	62.08	
10.50-10.99	10.68	29.06	11.00		25.60	59.75	
11.00-11.99	11.37	28.74	11.01		25.06	61.67	38.01
12.00-12.99	12.70	29.53	11.65		25.20	62.20	37.80
13.00-13.99	13.50	29.04	10.51		23.83	62.78	37.54
14.00-14.99	14.49	28.90	9.88		23.14	63.35	38.44
15.00-15.99	15.48	28.75	9.70		22.06	63.30	37.79
16.00-16.99	16.55	28.90	9.54		21.99	63.70	37.96
17.00-17.99	17.20	28.76	9.52		22.19	63.52	37.35
18.00-18.99	18.90	29.10	9.05		21.16	66.67	35.98

¹ Yolk-sac stage.

In order to study changes in body form during development, measurements were made on the following characters, using the cited reference points on cleared and stained specimens. (After ossifica-

tion of the premaxillaries all distances were measured from the most anterior point of the premaxillaries instead of the tip of the snout.)

Standard length: In early stage larvae, the distance from the tip of the snout to the tip of the notochord; after development of the caudal, the distance from the tip of the snout to the posterior edges of the hypural plates.

Head length: The distance from the tip of the snout to the cleithrum or pectoral girdle. The latter was chosen as a point of reference because the operculum cannot be easily distinguished until after ossification, and because the operculum extends posterior to the cleithrum in the later stages of the juvenile forms.

Snout to anus: The distance from the tip of the snout to the most posterior edge of the anus.

Snout to first and second dorsal fins: The distances from the tip of the snout to the origins of the dorsal fins. These measurements were made on larvae 11.0 mm. and longer, because the anterior spine in both the first and second dorsal fin was developed by this size.

Body depth: The vertical distance from the dorsal surface of the body directly above the dorsal point of the cleithrum to the ventral point of the cleithrum.

The relationships of the body measurements to standard length are shown as size on size regressions. In most instances the relations appear to be simple linear ones that can be fitted by the

TABLE 6.—Statistics describing the regressions of body proportions on standard length for Pacific mackerel

Independent variable x	Dependent variable y	Size of larvae (mm.)	\bar{x}	\bar{y}	N	b	a	$sy.x$
Standard length.	Head length.....	2.55-18.90	7.13	1.94	241	0.305	-0.234	0.128
Do.....	Distance snout to anus.	2.55-18.90	7.09	3.92	243	0.689	-0.965	0.267
Do.....	Distance snout to 1st dorsal.	11.15-18.90	14.83	5.60	26	0.362	0.241	0.170
Do.....	Distance snout to 2d dorsal.	11.15-18.90	14.70	9.56	26	0.665	-0.214	0.179
Do.....	Body depth.....	4.03-10.70	6.69	1.72	179	0.273	-0.111	0.123
Do.....	do.....	10.67-18.90	14.29	8.31	31	0.152	1.127	0.160

\bar{x} = mean of values of x .

\bar{y} = mean of values of y .

N = number of specimens examined.

b = rate of increase of y with respect to x .

a = y -intercept of regression line.

$sy.x$ = standard deviation from regression.

method of least squares. Statistics describing the regressions of body measurements on standard length are given in table 6. Slope b estimates the ratio of rates of growth of the individual measurements and standard length with reference to time. The curves of the confidence limits plotted for each regression line are based on 95 percent

accuracy and define the interval at any standard length within which each body measurement can be expected to fall for virtually all members of the population.

Head length

The head length increases by approximately 0.30 mm. for each millimeter increase in standard length. The range in sizes of the 241 specimens studied for this regression was from 2.6 to 18.9 mm. (fig. 5 and table 6).

Distance from snout to anus

The regression of this measurement on standard length is shown in figure 6 and statistically presented in table 6. Like the regression of head length on standard length, a straight line relation exists between this dimension and the standard length; the rate of increase being 0.69 mm. for each millimeter increase in standard length. Two hundred and forty-three specimens ranging from 2.55 to 18.9 mm. in length were measured for this regression.

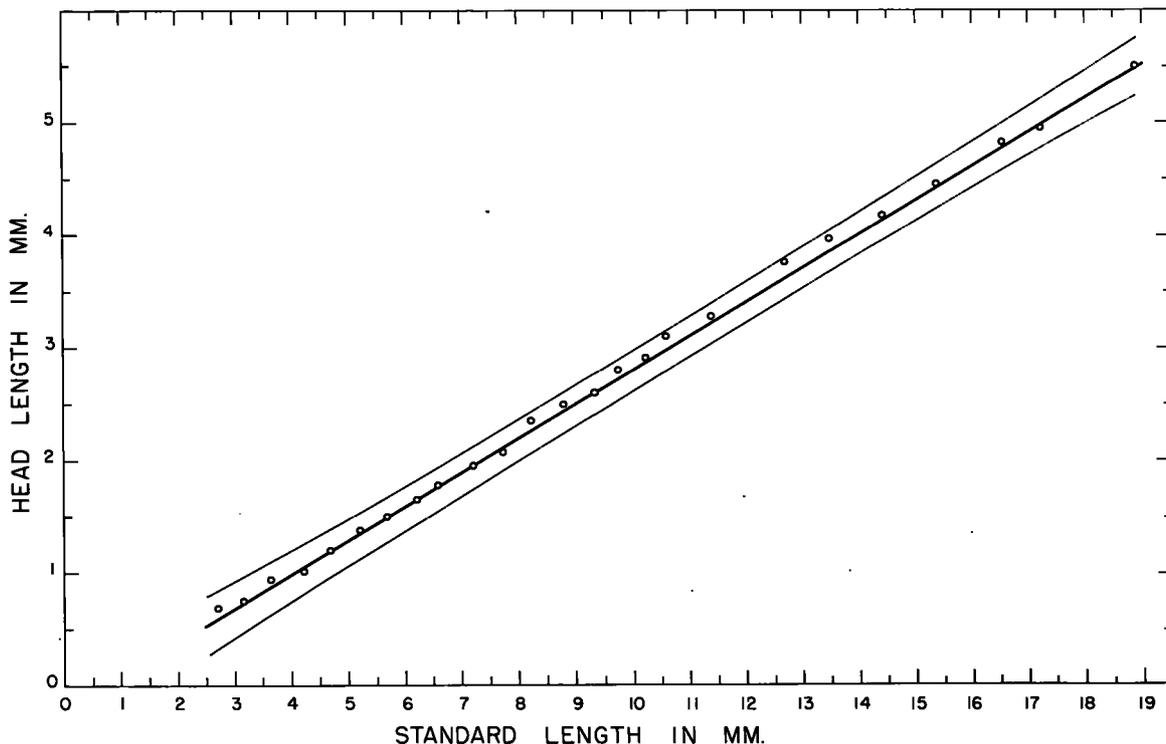


FIGURE 5.—Regression of head on standard length (middle line). The line is fitted to the data by the method of least squares, using all measured specimens. Each circle is the average of a group of measurements (see table 3, columns 2, 3, and 4). Statistics describing the line are given in table 6. The outer lines are the curves of 95 percent confidence limits.

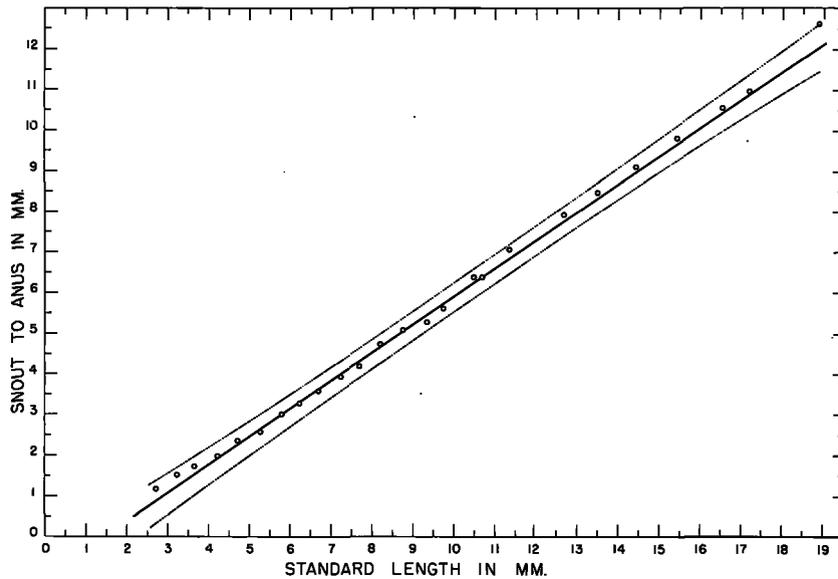


FIGURE 6.—Regression of distance from snout to anus on standard length (middle line). The line is fitted to the data by the method of least squares, using all measured specimens. Each circle is the average of a group of measurements (see table 3, columns 2, 3, and 7). Statistics describing the line are given in table 6. The outer lines are the curves of 95 percent confidence limits.

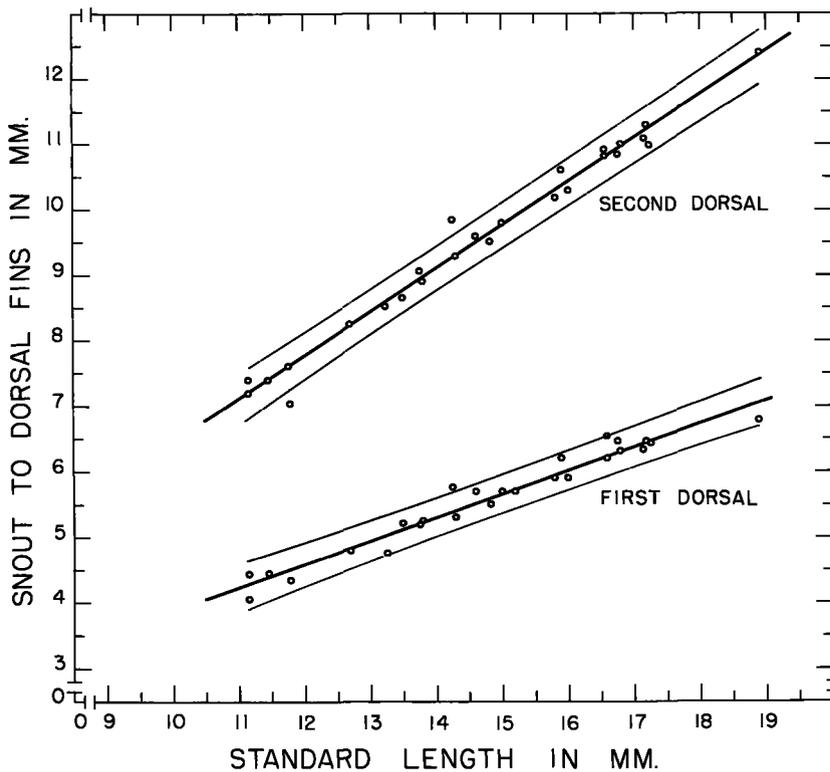


FIGURE 7.—Regressions of the distances from the snout to the first and second dorsal fins on standard length (middle line of each group). The lines are fitted to the data by the method of least squares, using all measured specimens. Each circle is the measurement from the snout to the origin of the fin (see table 3, columns 2, 3, 8, and 9). Statistics describing the lines are given in table 6. The outer lines of each group are the curves of 95 percent confidence limits.

Distance from snout to first and second dorsal fins

Regressions of the distance from the snout to the origins of the first and second dorsal fins on standard length show an increase in the snout to first dorsal dimension of 0.36 mm. for each millimeter increase in standard length, and in the snout to second dorsal dimension of 0.66 mm. for each millimeter increase in standard length. These two regressions are shown in figure 7. Twenty-six larvae, ranging in size from 11.2 to 18.9 mm., were measured for these regressions. Statistics describing the regression lines, fitted by the method of least squares, are presented in table 6.

Body depth (at pectoral)

The body depth of the Pacific mackerel, like that of the jack mackerel and hake, increases more rapidly in relation to the increase in standard length in the early part of larval development than in the late part. The Pacific mackerel, soon after the yolk-sac stage, becomes a deep-bodied, stubby form and then during the late larval period changes to a slimmer, fusiform shape. Although the hake is not fusiform in shape, it does become slimmer bodied as it increases in length. Oddly enough, the change in rate of growth of the body depth with respect to that of standard length takes place at almost the same length for the hake (at 10.6 mm.) and the Pacific mackerel (at 10.7 mm.). It might be assumed from these data that this change occurs at the time that the larva attains its juvenile shape. This change occurs very early in the jack mackerel (at 4.2 mm.), long before it attains juvenile size (Ahlstrom and Ball, 1954).

These facts may serve to further resolution of the argument as to when a larva becomes a juvenile or may only cloud the issue. As noted, a change in body shape in Pacific mackerel and hake occurs at about 10.5 mm. in length. The larva then attains the fusiform shape characteristic of the juvenile and adult stages. An argument could be advanced to support the idea that the juvenile stage begins at the size when this shape is attained. Other arguments, however, can be given in support of the fact that the juvenile stage is not attained until the completion of fin formation. Some of the features that characterize juvenile Pacific mackerel and hake, such as the fusiform or slimmer shape, are attained earlier than other features such as the completion of fin formation.

The body depth of the early stage Pacific mackerel larvae increases at a rate relative to the standard length, which is almost twice that of the late stages. Measurements were not made for body depth in the yolk-sac stages; no larvae were measured until they were 4.0 mm. in length, or longer. This was assumed to be a size at which the yolk sac would be completely absorbed. Two hundred and ten specimens were measured, of which 179 were in the early stage to 10.7 mm. in length, and 31 larvae were in the later stage ranging in size from 10.7 to 18.9 mm. in length. The rate of increase in body depth during the early stage was 0.27 mm. for each millimeter increase in standard length, and during the late stage it was 0.15 mm. for each millimeter increase in standard length (fig. 8; table 6).

SEQUENCES OF OSSIFICATION

There are no ossified structures in the larva of the Pacific mackerel at hatching. The sequences of ossification can best be shown by the chart method (fig. 9) devised by Ahlstrom and Counts (1955). Ossification of the cleithrum occurs very soon after hatching, thus facilitating the measurement of the head. In the head region, the sequence in which ossification is initiated is as follows: first the cleithrum and parasphenoid, then the premaxillaries, mandibles, and teeth. These appear at about 3.0 to 3.5 mm. The following begin to ossify in the sequence noted, before the larva is 6.0 mm. in length: branchiostegal rays, lower limb of the gill arch, preoperculum, bones of the occipital region, interoperculum, and suboperculum.

Discussions concerning ossification of bones in the head are kept to a minimum and restricted only to those structures which are readily visible without dissection. If the descriptions of sequences of ossification in the rest of the body are relatively more detailed, it is because the processes of development of those parts are easily seen in the stained specimens, and their more detailed descriptions may serve, in part, to resolve some of the questions not adequately investigated by other workers. Such questions are discussed later in the descriptions of the interneurals of the dorsal fins and finlets, the caudal keels, and some of the vertebral parts.

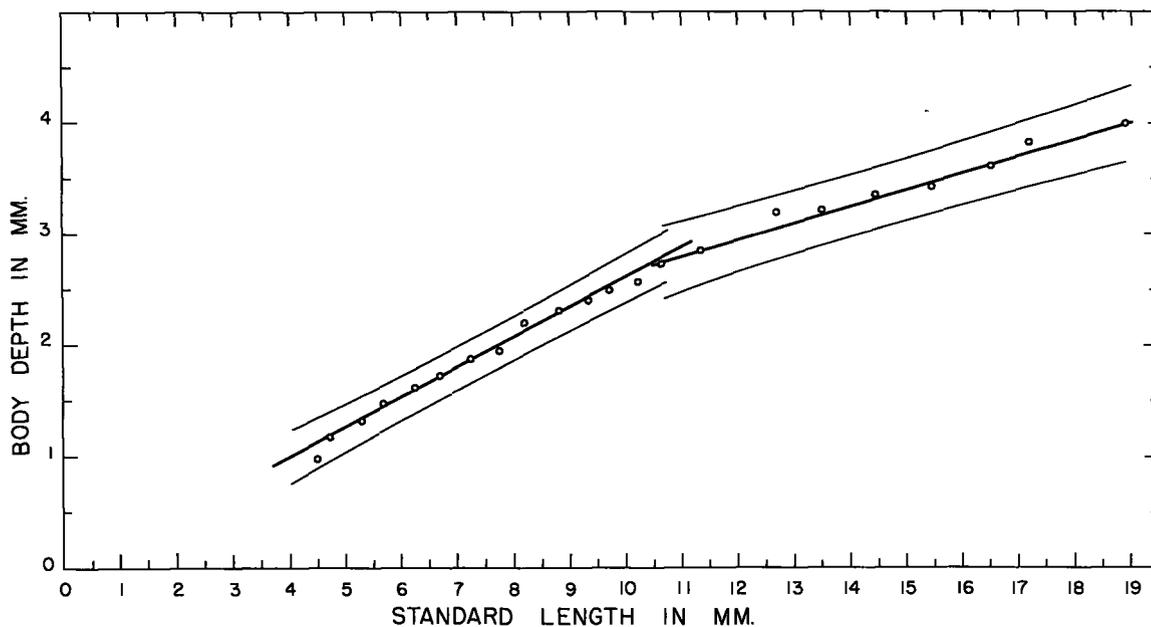


FIGURE 8.—Regressions of body depth (at pectoral) on standard length (middle line of each group). The lines are fitted to the data by the method of least squares, using all measured specimens. One line is for larvae 4.03 to 10.70 mm. in length, the other for larvae 10.67 to 18.90 mm. in length. Each circle is the average of a group of measurements (see table 3, columns 2, 3 and 6). Statistics describing the lines are given in table 6. The outer lines of each group are the curves of 95 percent confidence limits.

Teeth

The teeth of the adult Pacific mackerel are thin, conical projections situated in a single line on each of the premaxillaries and mandibles. Teeth first appear on the most anterior section of the premaxillaries and mandibles at about 3.5 mm., almost at the same time that the yolk sac is absorbed. Additional teeth are added progressively posterior to the first ones. Smaller teeth also form between these, each in a horizontal position either anterior or posterior, or both, to those present. Each of these points inward toward its larger neighbor. These horizontal teeth rise into place to point vertically from their respective bases. Between these groups, more single teeth may begin to grow by themselves. These latter teeth grow straight from their bases. The final result is a more or less even spacing of single teeth posteriorly and groups of two or three teeth and single ones laterally and anteriorly. The teeth are recurved anteriorly and tend to become nearly straight in the posterior sections of the jaws. Those in the most posterior section tend to recurve posteriorly. There are usually one or two more teeth on the mandible than on the premaxillary

in specimens between 8.45 and 30.0 mm., as is shown in the following tabulation:

Size of larvae (mm)	Count of teeth on one side	
	Premaxillary	Mandible
3.42	1	1
4.67	3	3
5.68	4	4
6.62	6	6
8.45	7	8
10.30	8	9
11.16	10	12
13.50	11	12
17.15	13	15
24.6	17	19
30.0	20	22
66.6	34	27

Two or three palatine teeth appear at about 13.5 mm. Development of palatine teeth is not very rapid; only three teeth are present in the 16- to 18-mm. sizes. By the time the juvenile is about 30.0 mm. in length there are about 14 teeth on each palatine. The counts were not determined beyond this size.

The time of the development of the vomerine teeth is unknown; two were seen in the 66.6-mm. specimen.

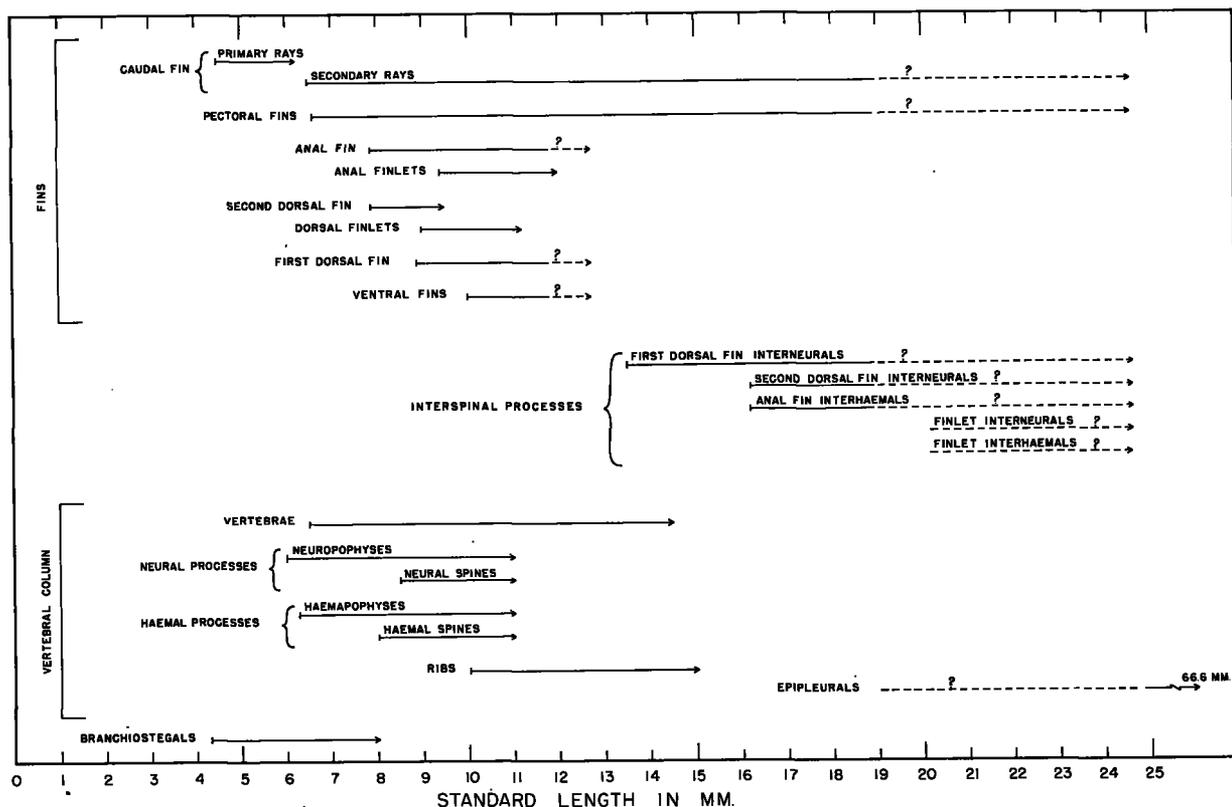


FIGURE 9.—Diagrammatic summary of the sequences of ossification of basic meristic structures and their parts in Pacific mackerel larvae and juveniles. Progressive ossification is indicated by the lines and the symbols attached to them: vertical bars, beginnings of ossification; solid lines, serial growth and additional numbers; broken lines and question marks, absence of specimens in series where growth and numbers are known to increase; arrows, achievement of final counts and continued growth (see table 4).

Branchiostegal rays

The total number of branchiostegal rays per side in the Pacific mackerel is invariably seven. The first branchiostegal rays appear postero-ventral to the eyes at about 4.3 mm., and succeeding rays form successively anteroventrad until the full complement of seven rays on each side is achieved at about 8.0 mm. (fig. 9).

Gill rakers

The gill arches appear in the Pacific mackerel at about the same size as do the branchiostegal rays. This takes place about 4.5 to 5.0 mm. The first ossification of the gill rakers is seen when they appear at about 6.6 mm. on the lower limb of the first gill arch. A tabulation of the gill raker counts from ten specimens up to 30.0 mm., one 66.6 mm. specimen, and an adult 241 mm. in length follows.

The gill raker located at the angle between the

upper and lower limbs of the gill arch articulates on a small bone which is connected to the two limbs by cartilage.

Size of larvae (mm.)	Gill raker counts		
	Upper limb	Angle	Lower limb
6.62.....	0	0	6
8.89.....	0	1	8
10.03.....	0	1	8
11.16.....	1	1	11
13.24.....	1	1	11
17.15.....	2	1	13
17.20.....	2	1	14
17.24.....	2	1	15
24.6.....	5	1	18
30.0.....	7	1	19
66.6.....	9	1	23
241 (adult).....	12	1	28

Fin formation

The sequence of fin formation in Pacific mackerel larvae is similar to that in jack mackerel larvae, but quite different from the sequence in hake larvae. In all three species, the larval pec-

torals without rays are the first fins to form, followed by ray formation in the caudal fin. Larvae of Pacific mackerel and jack mackerel next initiate pectoral ray development, but development of rays in the pectoral fins of hake larvae is delayed until its other fins are formed. Ventral fins form early in hake larvae, on the other hand, whereas they form late in Pacific mackerel and jack mackerel. The order of fin formation in these three species is shown in the following tabulation:

Order of first appearance of fins

Order of formation	Pacific mackerel	Jack mackerel ¹	Hake ²
1.....	Larval pectorals (without rays).	Larval pectorals (without rays).	Larval pectorals (without rays).
2.....	Caudal.	Caudal.	Caudal.
3.....	Pectorals (with rays).	Pectorals (with rays).	Ventrals.
4.....	Second dorsal. ³ Anal. ³	Second dorsal. ³ Anal. ³	First dorsal.
5.....	Dorsal finlets. ³ Anal finlets. ³	First dorsal.	Second dorsal. ³ Anal. ³
6.....	First dorsal.	Ventrals.	Pectorals (with rays).
7.....	Ventrals.		
8.....	(Caudal keels).		

¹ Ahlstrom and Ball (1954).

² Ahlstrom and Counts (1955).

³ Simultaneous formation by ossification.

The early development of the caudal fin in all three species of larvae undoubtedly results from the important role played by this fin in larval propulsion. Larval fish are observed to move by constant lateral wiggling and sculling of the tail. In all three species, development of the second dorsal and anal fins begins simultaneously. Several structures develop in Pacific mackerel larvae that have no counterparts in the other species, particularly the dorsal and anal finlets and the keels on the caudal peduncle. The latter were designated as pseudofins by Herald (1951) when found on juvenile scombrids. Each of these keels is made up of a series of scales arranged in such a fashion that cursory examination would have them appear as rays. For this reason they are included in the list (in parentheses), and their development is discussed after that of the true fins.

Caudal fin and its association with the vertebral column.—The actinotrichia of the caudal fin appear soon after hatching, originating at the tip of the tail and extending almost one-fourth of the way into the caudal fin fold. They extend to the edges of the fin fold at about 3.5 mm. Ossification of the rays begins ventral to the tip of the tail. Their midline is clearly discernible by reason of

the larger space between the first two major rays that are formed. These two ossified rays appear at about 4.5 mm. The tip of the notochord turns dorsad at about 6.0 mm., pulling up the rays toward a horizontal position and gradually aligning their midline with the body midline. This final alignment occurs at about 6.8 mm. There seems to be an even rate of ossification in the rays of the dorsal and ventral halves of the tail until after the midlines of the tail and body are aligned.

The Pacific mackerel has 17 major rays in the caudal fin: 9 dorsal and 8 ventral to the midline of the fin. The final count is achieved at about 6.5 mm. There was no variation in this number and order in any of the larvae or juveniles which had developed their full complement of major rays.

The secondary rays of the fin begin to form at about 6.5 mm. (fig. 9), almost as soon as the full complement of the principal rays has been achieved. Secondary rays form slowly, and the final count of 10 to 11 dorsal and ventral rays is not achieved until some length between 18.9 and 24.6 mm. (fig. 9). The 18.9 mm. specimen had 9 secondary rays in each section, and the one 24.6 mm in length had 11.

In the dorsal half of the caudal fin, eight principal rays are associated with the large, dorsal, hypural plate, and the ninth ray with the small, upper hypural. Below the midline of the caudal fin, six principal rays are associated with the large ventral, hypural plate, and the seventh and eighth rays with the lower hypural. The secondary rays of the dorsal half of the fin are associated with the two epurals and the modified neural process of the penultimate vertebra. The ventral, secondary rays are associated with the modified haemal processes of the ultimate and penultimate vertebrae.

A constant number of 17 principal rays in the caudal fin is found in many percomorph fishes, including scombrids. It was noted in all material studied that the complete complement of principal rays was formed before the secondary rays began to develop. This sequence, shown in the figures illustrating larval development in Roedel's paper (1949a) on the life history of the Pacific mackerel, may be in error on this point. The figure of the 8 mm. larva has only eight major rays in the dorsal half of the fin, with two dorsal,

secondary rays already developed. The illustration of the major rays of the caudal fin in the 11 mm. larva is in error. This one is shown as having only 13 major rays: 6 dorsal and 7 ventral.

Pectoral fins.—When the larva is about 3.5 mm. in length and the yolk is about two-thirds absorbed, the pectoral buds can be seen (fig. 2c). They become functional at about the same time that the yolk is absorbed. The rays begin to ossify at about 6.6 mm., appearing first in the upper or dorsal section of the fin. Ray formation continues ventrally until the full number of 19 to 21 rays is achieved. Again, because of the lack of specimens between 18.9 and 24.6 mm., the size at which the total number is reached is unknown (fig. 9). The 18.9 mm. specimen had 18 pectoral rays, and the 24.6 mm. specimen had 19 pectoral rays. Most of the older specimens examined had one more ray developed on the right pectoral fin than on the left. The following list of 11 selected larval and juvenile specimens and an adult shows this variation:

Standard length (mm.)	Pectoral fin rays	
	Left fin	Right fin
6.6	5	5
7.9	7	7
8.7	9	9
9.4	9	9
10.7	10	10
13.8	13	14
14.8	15	16
15.8	17	18
18.9	17	18
24.6	Broken	19
30.0	20	21
241 (adult)	19	-----

The first dorsal, anal, and ventral fins had their full complement of spines and rays developed in the 12.7 mm. specimen, the only one of its size group.

The anal and second dorsal fins begin to form at the same time, at about 7.9 mm. Since differentiation of spines and rays is difficult in the early stages of ossification, the ossified parts are recorded as rays (table 4).

Anal fin.—The first rays of the anal fin appear in a group of ten at about 7.9 mm., ventral to the area between the haemal processes of the 16th and 20th vertebrae. Rays continue to form anteriorly and posteriorly until the second spine is formed ventral to the haemal spine of the 16th vertebra. The last ray is formed ventral to the haemal

spine of the 21st vertebra. The anterior spine does not ossify until after all of the anal finlets are formed, thus probably completing the fin at about 12.0 mm. (fig. 9). The difference in the size of the two anal spines is quite marked. The first spine becomes a very strong, recurved structure, whereas the second spine is a weak one, hardly discernible from the rays of that fin except by the fact that it is not segmented. Clothier (1950) recorded the variation in anal fin rays as nine to thirteen.⁴ Every specimen studied here (table 4; appendix), having its full complement of rays, had eleven.

Second dorsal fin.—The first group of six rays of this fin appears in the area dorsal to the neural processes of the 16th and 20th vertebrae at about 7.9 mm. As in the anal fin, additional rays develop anteriorly and posteriorly until the final count of I, 10 or 11 is reached at 9.5 mm. (fig. 9). A variation of one ray was recorded for only one specimen in all of those developed far enough to have their full count (table 4). Clothier's counts (1950) of the second dorsal fin varied from I, 9 to 13.⁵ Unlike the anal fin, the total count of the second dorsal fin is reached usually before all the dorsal finlets are formed. In one instance, the full complement of I, 11 appeared in a precocious specimen, 8.67 mm. in length. The first spine is dorsal to the neural process of the 15th vertebra and the 11th ray is dorsal to the neural process of the 21st vertebra. The spine in the second dorsal fin is a weak one like the second spine in the anal fin.

First dorsal fin.—The anterior six spines of the first dorsal fin appear at about 8.9 mm., dorsal to the area between the third and seventh neural processes. The remaining spines form posteriorly until the full complement of 9 or 10 is reached at some size between 11.8 and 12.7 mm. (fig. 9). Only one specimen with fully developed anterior dorsal spines had 9 spines, all others had 10. Clothier (1950) recorded a total count of nine spines in the first dorsal fin of the Pacific mackerel. The tenth spine in his specimens might have been overlooked, since it barely protrudes from between the posterior edges of alate structures in

⁴ Fitch reports valid anal counts of 10 to 12 rays (by correspondence).

⁵ Fitch reports second dorsal counts of 10 to 13 (by correspondence).

the dorsal slot and lies in the shallow, midsection of the slot (fig. 11).⁶

The ventral fins.—The last of the major fins to begin formation are the ventrals. These are located in the thoracic region, and begin to form at about 10.0 mm. They are complete with their full count of I, 5 at some size between 11.8 and 12.7 mm. (fig. 9).

Finlets.—Further subdivision of the median fins, beyond the formation of the two dorsals, continues with that of the dorsal and anal finlets. Each finlet, except the most posterior one, forms first as a single ray and then becomes a short, multibranching affair on a single base. The final count of the finlets in initial development has one-half ray added to it (table 4; appendix) because the last finlet is formed of two separate rays, the posterior one shorter than the one preceding it. These two rays join on a single base (figs. 4, 11). The formation of the dorsal finlets may begin as early as 9.0 mm., sometimes, but not usually, before the second dorsal fin is complete at about 9.5 mm. The full complement of six finlets is reached at about 11.2 mm. The anal finlets begin to form at about 9.4 mm. and are complete at about 11.5 mm. In consideration of the differences in rate of development in larval fishes, it may be assumed here that the dorsal and anal finlets start to form and are completed at about the same stage (fig. 9).

Discussion of fin counts.—Clothier's anal fin count (1950) for the Pacific mackerel was recorded as I-I,9 to 11. In his introduction he explained his method of fin counts as follows: "A comma separates the spine number from the ray number in the same fin. In the case of two dorsal fins, a hyphen separates the individual counts of the two separate fins." It is evident, from the hyphenated separation of the first two spines of the anal fin, that he regarded the first spine as one that is entirely separated from the rest of the fin. This can be very easily assumed if no attempt is made to study the interhaemal system of this fin. Such examination shows that the interhaemal of the weak spine of the I,9 group is fused to that of the strong spine (fig. 11) separated by Clothier. He used a hyphen probably on the basis of the fact that externally, the strong spine does

stand slightly apart from the rest of the fin and is not connected by a membrane. Kishinouye (1923) also mentioned an "isolated spine" in the anal fin of the Japanese mackerel, *Scomber japonicus*, now *Pneumatophorus japonicus*, I have had no opportunity to examine any of that species, but it is likely that the "isolated spine" is the same as the strong one in the Pacific mackerel and that it is directly associated in the interhaemal system in the same way.

It is my opinion that the separation of fin counts by a hyphen should be made only if the interspinal parts or groups are entirely separated from one another as in the distinct separation of the first dorsal from the second dorsal fin; the dorsal finlets from the second dorsal fin; and the anal finlets from the anal fin.

Caudal keels

Herald's study (1951) of the components of the lateral ridges on the tails of young scombroid fishes led him to conclude that they were rays, and therefore parts of what he chose to name "pseudofins," or "false fins." He further stated that several specimens of *Auxis thazard* were examined for him by Charles Wade, of the Philippine Fishery Program, who said that he believed that there was an indication that these false fins were in the process of being lost when the fish was about 200 mm. in length. Cleared and stained small specimens and the tail sections of larger fishes would have shown that during keel development, the so-called rays were being covered by flesh and skin, and instead of being lost, were merely obscured.

It is my choice, here, to call the lateral ridges the caudal keels, a term used by many taxonomists when defining these structures. The term "rays," used by Herald for the individual parts of the keels, is inappropriate because they are actually modified scales. This is revealed, even in the early stages, when the keel is dissected away from the tail and its parts are separated, as is illustrated for the Pacific mackerel in figure 10. *Auxis* species also has the same type of scales which are thinner, more numerous, and in several rows.

Wade thought that these scales in *Auxis* were disappearing, probably because only the tips of a few of them could be teased apart at the tops of the keels. On examination of a large specimen of

⁶ Fitch reports counts of 9 to 11 spines, and claims that no spine was overlooked, but it was obvious that some were overgrown with integument (by correspondence).

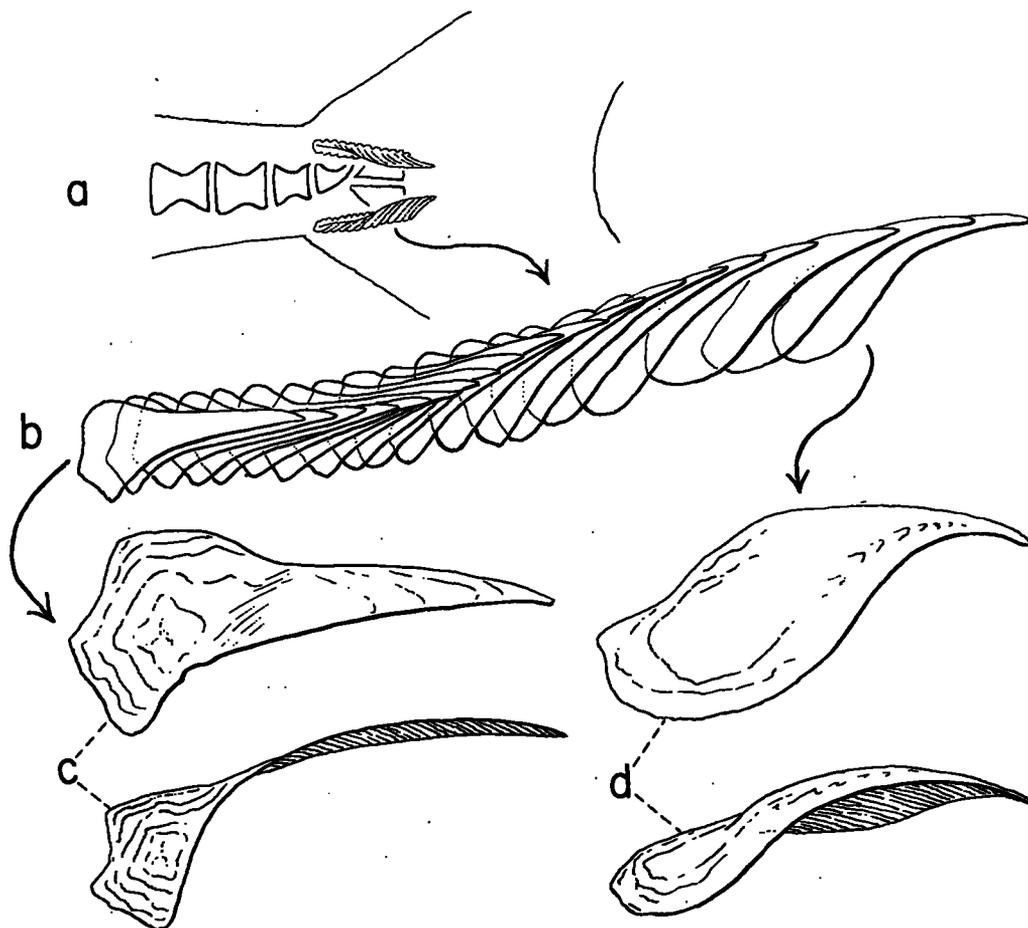


FIGURE 10.—The caudal keels and the scales of the ventral keel on the tail in the Pacific mackerel; from a specimen 66.6 mm. long. *a.* Positions of the keels on the left side of the tail (not accurate for counts). *b.* Detail of the arrangement of the scales on the ventral keel. *c.* and *d.* Plane and lateral views of the first and last scales, respectively.

Auwis sp. (370 mm. fork length).⁷ I found these tips much in evidence even in so large a specimen, indicating that the growth over the scales proceeded only to a certain point and no farther. In the adult Pacific mackerel, however, the caudal keel scales do not become covered except for a slight overgrowth at their bases. The rigidity of these keels is maintained by membranes between the scales.

Material showing the initial ossifications of the caudal keel scales in the Pacific mackerel is absent from our collections. The first specimen showing the scales was 48.7 mm. in length. The drawings illustrating the keels and the arrangement of their

scales were made from a specimen 66.6 mm. in length. The following is a list of these two specimens and one adult showing the counts of the scales on all of their keels:

Length (mm.)	Left side		Right side	
	Dorsal	Ventral	Dorsal	Ventral
48.7.....	23	19	20	20
66.6.....	23	19	21	18
235.0.....			24	23

No counts were made for the left side of the 235.0 mm. specimen, because it had been removed and discarded before the keel studies were undertaken.

⁷ Loaned to the U.S. Fish and Wildlife Service by the Inter-American Tropical Tuna Commission.

There are two keels on each side of the tail of the Pacific mackerel (fig. 14a). One of these is dorsal, lying longitudinally over the area of the dorsal sections of the urostyle and the dorsal hypural plate and approximately over the bases of the secondary and upper primary rays of the caudal fin. The other, the ventral keel, lies longitudinally over the area of the lower hypural and the posteroventral section of the adjacent, ventral hypural, and approximately over the bases of the ventral, secondary, and lower, primary rays of the caudal fin.

The complex curve of each keel is the sum of the curves of the individual scales which form the keel (fig. 10). It is difficult to distinguish the complexity of this structure and its parts until they are separated from the tail and from each other. Ossification of the scales is heaviest on their trailing edges with partial ossification of the leading edges near their bases. The remainder of each leading edge seems to remain unossified and flexible throughout further development and growth.

The median keels found on the caudal peduncles of most scombrid fishes are absent in *Pneumatophorus* spp., *Scomber* spp., and *Rastrelliger* spp. These keels, unlike the ones described above, do not have scales. Herald (1951) cited this fact for *Auaxis thazard*, and Godsil (1954) stated that in this species the lateral enlargement of the apophyses on the 32d through 34th vertebrae constitutes the principal portion of the median keels. In addition to the support of the keels by the apophyses in the adult *Auaxis*, there is also a cartilagenous-like edge overlying each median keel from anterior to posterior, which appears in the preserved specimen as a distinct, yellow ridge.

The function of the median keels in the scombrids is immediately apparent when examining a specimen of *Auaxis*. The caudal peduncle is so flattened by lateral growth and so sharply edged with cartilage that these keels can serve no other purpose than that of cutting water and lowering resistance during rapid tail movement. This horizontal flattening of the caudal peduncle with a vertical tail is analagous to the vertical flattening of the caudal peduncle in combination with the horizontal flukes in the porpoise.

The possible functions of the two lateral sets of keels in the scombrids are open to conjecture because of their size, their position, and their align-

ment. Three possibilities suggested during this study are as follows: (1) they support the bases of the caudal fin rays which would be under great stress at those points during very rapid movement of the tail, (2) they offer additional surface area to increase water resistance and aid in rapid swimming, and (3) their slightly oblique alignment and curve may aid in diving and upward swimming movements, in that their small size in relation to the bulk of the fish may be similar to the small size of the diving planes on a large submarine.

Interspinal systems

The association of the two dorsal fins, the anal fin and the finlets with the vertebral column is by means of the interneurals dorsally and the interhaemals ventrally (fig. 11). The interneurals begin anteriorly between the second and third neural spines and the interhaemals begin in front of the first haemal spine. Both of these groups terminate posteriorly in the sections between the 25th and 26th neural and 11th and 12th haemal spines, respectively. At about 13.7 mm., the anterior 3 or 4 interneurals of the first dorsal fin begin to ossify. The interspinal systems of the second dorsal and the anal fins begin to form at about 16.5 mm. as a group of 5 or 6 ossifications about mid-length of their respective fins. The time of the appearance of these structures for the finlets is not known, because they were almost completely developed in a specimen 24.6 mm. in length, but not present in an 18.9 mm. specimen. Since the interspinal bones of the first dorsal, second dorsal, and anal fins appeared in the same sequence as did the spines and rays, they can be assumed to develop in the same orders as those of their external structures.

Each spine, ray, and finlet can be said to be the posteriorward, exterior projection of its interspinal bone, or conversely, each of these exterior ossifications can be said to have an inward extension, pointed forward into the body to terminate between vertebral processes. Each interneural and interhaemal serves two functions: it connects, as a support, directly to a fin ray or spine, and serves as a base for the articulation of the adjacent anterior ray or spine (fig. 11).

When their ossification is completed, the interspinal bones of the second dorsal and anal fins and the dorsal and anal finlets may be said to be

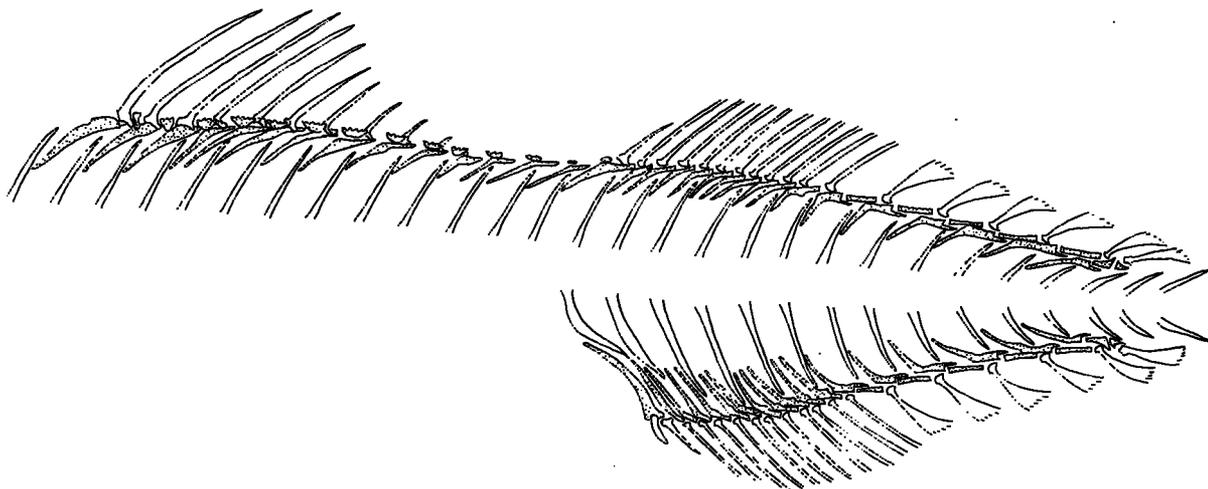


FIGURE 11.—Arrangement of the parts of the dorsal and anal fins and finlets, their interspinal bones and the vertebral spines (2d to 29th neural and 1st to 15th haemal) in the Pacific mackerel; from a specimen 66.6 mm. long (see figs. 12, 13 and 14).

mirror images of one another (fig. 11). The descriptions of the interneurals of the second dorsal fin and of those of the dorsal finlets can be regarded as the same in their anal counterparts. The only differences are as follows: (1) the interneural of the first spine of the second dorsal fin is in two parts with a span of almost 3.5 vertebral lengths, whereas the interhaemal of the first spine of the anal fin is a single ossification extending almost vertically in front of the first haemal spine; (2) there is no fusion of the interneurals of the second dorsal fin, whereas the interhaemals of the first two spines of the anal fin are fused; and (3) there are no anterior keels on the interhaemals of the anal fin.

Dorsal fin interneurals.—Although the first and second dorsal fins are not continuous, the interneurals are (fig. 11). If the intermediate spines were present and the two dorsal fins and the finlets were regarded in entirety as a single fin, it would be seen that there is one more exterior ossification than there are interneurals (33 in spines, rays, finlets, and 32 in interneurals). This difference in count is also found in the anal fin (19 in spines, rays, and finlets, and 18 in interhaemals). In the first dorsal fin, the proximal section of the interneural of the second spine is fused to the interneural of the first spine, as is the case with the fusion of the interhaemals of the first two spines in the single anal fin.

The intermediate spines between the first and second dorsal fins are present in *Auris* species and are very clearly defined as early as 28 mm. They become embedded in the adult of that species.

In the Pacific mackerel, each interneural of the "single" dorsal fin is made up of two sections: (1) distal, near the base of the ray, spine, or finlet, and (2) proximal between the distal section and the vertebral column. The modifications of these interneural sections are discussed separately under their descriptions for the individual divisions of the dorsal fins and finlets.

Eaton (1945) defined these structures as pterygiophores, and their parts as proximal, middle, and distal radials. He did not accept the terms "baseost" for the distal section or "axonost" for the proximal section, or the term "interneural." In the latter case, his reasoning was based on the fact that in some fishes these bones do not extend so far as to terminate between the vertebral spines. The terms "interneurals" and "interhaemals" will be used here because in all cases they do extend so far, and their meanings are quite clear both by context and illustration (figs. 11 and 13). It was his theory, derived from other studies of the skeletons of fossil fishes, that the phylogenetic development of these bones began with three sections. This evidence was, in part, borne out by his investigations of the interneurals of the contemporary primitive fishes, *Amia*, *Acipenser*, and *Salmo*, and

of an advanced percoid fish, *Tilapia macrocephala*. His illustration of a spine and interneural in *Tilapia* showed the same condition as that discussed and illustrated for the two-part system of the intervertebrals in the Pacific mackerel. However, he also showed that the middle part is fused onto the distal end of the proximal section of the interneural. This is probably true for all of the proximal sections discussed below.

The three-part system may be indicated in Pacific mackerel by the symmetrical and opposite positions of small holes on the proximal sections of the dorsal and anal finlet interspinal bones. Such holes are also present near the angles of the single interspinals of the anal and second dorsal fins, indicating the possibility of at least two parts in these bones. The shapes of the more anterior proximal sections of the finlet interspinals and the single anal and second dorsal interspinals bent almost at right angles (fig. 11), may also indicate the possibility of two bones fused together to form such angles. Another example that may be used to corroborate this theory is the three-part system of the last finlet interneural. The argument may withstand criticism by the fact that a point of articulation for the last finlet might just as well have been on the middle section, thus making out a distinct two-part instead of a three-part system. Criticism against this, on the other hand, may be that the last bone is an indication of an incomplete neural system which would have been present as a support for the one-half ray of the last bifurcate finlet (table 5). Because there are only two clearly defined parts in these systems and their modifications (except in those of the last finlets and the single interspinal bones of the second dorsal and anal fins), all of the Pacific mackerel interspinal structures will be regarded here as made up of two parts, or one part derived from the fusion of two.

As mentioned above, there is a space between the two dorsal fins in which there are several interneurals that bear no spines. Murakami and Hayano (1956) made use of this character in separating *P. japonicus* and *P. tapeinocephalus*. They found that the two species had a different number of spines in the first dorsal fin in relation to the total number of interneurals associated with this fin and the section bearing no spines. Their illustration of each fish included the second dorsal

fin spine and two interneurals of the second dorsal fin. The anterior one of these interneurals, which is included in their counts, belongs to the second dorsal fin spine (see following paragraph and fig. 11). Their valid counts, therefore, include one more interneural than is correct if, as it seems, they did not intend to include any belonging to the second dorsal fin.

Abe and Takashima (1958) separate *P. japonicus* and *P. tapeinocephalus* distinctly on the basis of number and position in the proximal segments of the interneurals. In *japonicus*, their counts for species are about the same as those of Murakami and Hayano (1956) with a different method of counting in that they recognize the last interneural of the spinous dorsal and section with no spines as I described it. Their second method of differentiation is based on the numbers of proximal segments of the first dorsal fin between each successive pair of neural spines beginning with numbers 2 and 3. The patterns of numbers of interneurals (1, 2, or 3) between successive pairs of neural spines for 6 or 7 pairs (p. 3, table 7) show differences for each species, with no overlap. The count of interneurals by this system could be "2" for the first one since it is a bone composed of the two fused, proximal segments belonging to the first and second spines. The authors are correct, however, in simplifying this to a count of "1" in order to avoid confusion.

These investigators describe as "middle segments" the parts I have called "distal" in the interneurals of the first dorsal and the section with no spines. The middle segments of the second dorsal are described as, " * * * single, rounded, semi-transparent cartilagenous balls * * * each clipped by the root of each half of each soft-ray." They do not explain where "distal" or third segments are located in either dorsal fin. If my theory of the fusion of middle and proximal segments is correct, it is obvious that calling the distal segments "middle" may be due to these investigators not having larval and juvenile specimens for study. Many incorrect conclusions can be made when only adult specimens are studied. This is shown later in my discussion of why some neural spines seem to be based on the middle of their centra and might be assumed to have originated there, and why Kishinouye (1923) assumed that there were no parapophyses on the anterior vertebrae.

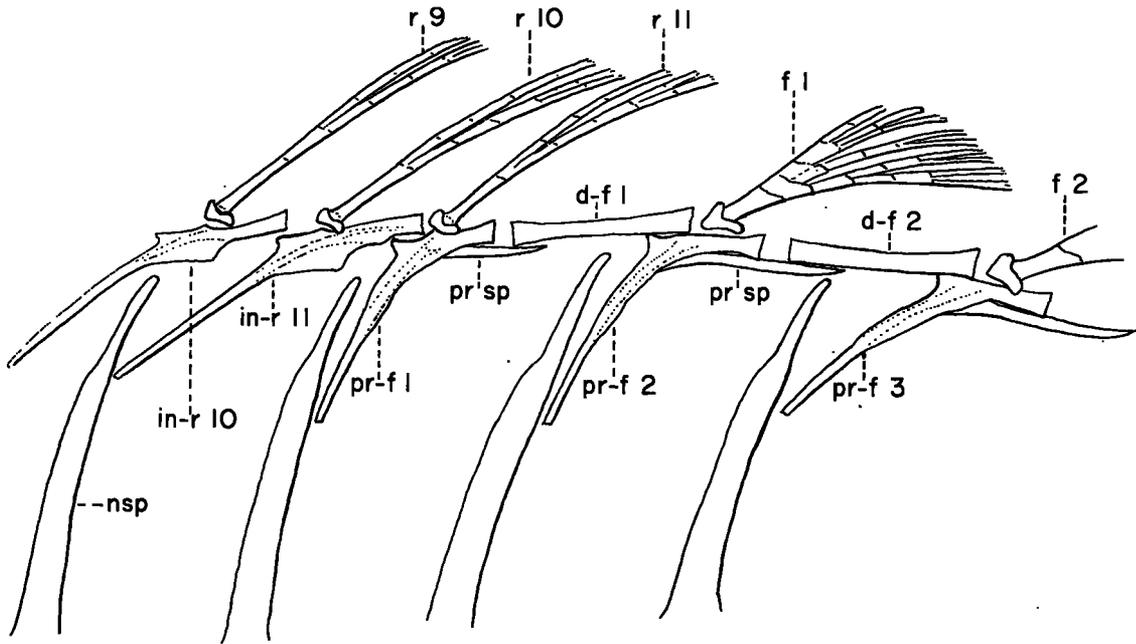


FIGURE 12.—Detailed lateral view of the arrangement of the last three rays of the second dorsal fin, the first two finlets, their interneurals, and the neural spines in the Pacific mackerel; from a specimen 66.6 mm. long (fig. 11); *d-f* 1 and 2, first and second finlets; *in-r* 10 and 11, interneurals of the 10th and 11th rays; *nsp*, neural spine; *pr-f* 1 through 3, proximal sections of the first through third finlets; *pr sp*, spine on the proximal section; *r* 9 through 11, ninth through eleventh rays.

Second dorsal fin interneurals.—The posterior end of the proximal section of the interneural of the spine of the second dorsal fin lies almost two-thirds of the length of one vertebra in front of its distal section. The outline of a cartilaginous attachment can be discerned in older specimens, connecting the posterior end of the proximal section to the short ossification of the distal section that appears directly in front of the base of the spine. This stubby little bone is a nonserrate, non-alate modification of the distal section in the two-part system of the first dorsal fin interneurals (see first dorsal and finlet interneurals). The base of the spine lies over the forward section of the 17th vertebra and the distal base of the proximal section of the interneural lies above the center of the 16th vertebra. This section points forward to terminate behind the spine of the 13th vertebra. The span of this single interspinal system is approximately three vertebral lengths. The interneurals of the 1st to the 11th rays are horizontal for a short distance forward of their rays and then bend at an angle which becomes less acute as they progress posteriorly. The bifurcate base of each

ray articulates on the almost horizontal section of the interneural belonging to the ray behind it. The forward lying interneural of the first ray develops narrow anterior and posterior keels. The interneural of the second ray has rather wide anterior and posterior keels. Proceeding posteriorly, the keels become narrower and smaller, and are finally restricted to the posterior obtuse angle of the interneurals. The interneurals in the posterior section of this group have no keels.

Finlet interneurals.—The interneural of each finlet is divided into two parts, one behind the other, connected by cartilage (fig. 12). The two sections seem to present an exploded and extended view of the single interneurals of the second dorsal fin rays. This condition of two-part interneurals exists in three sections of the total "single" dorsal fin: the first dorsal fin, the section bearing no spines, and the finlets (fig. 11). It can be seen here that the single interneurals of the second dorsal fin are the result of the fusion of the two-part system. This is most easily seen in the last interneural of the dorsal fin (fig. 12).

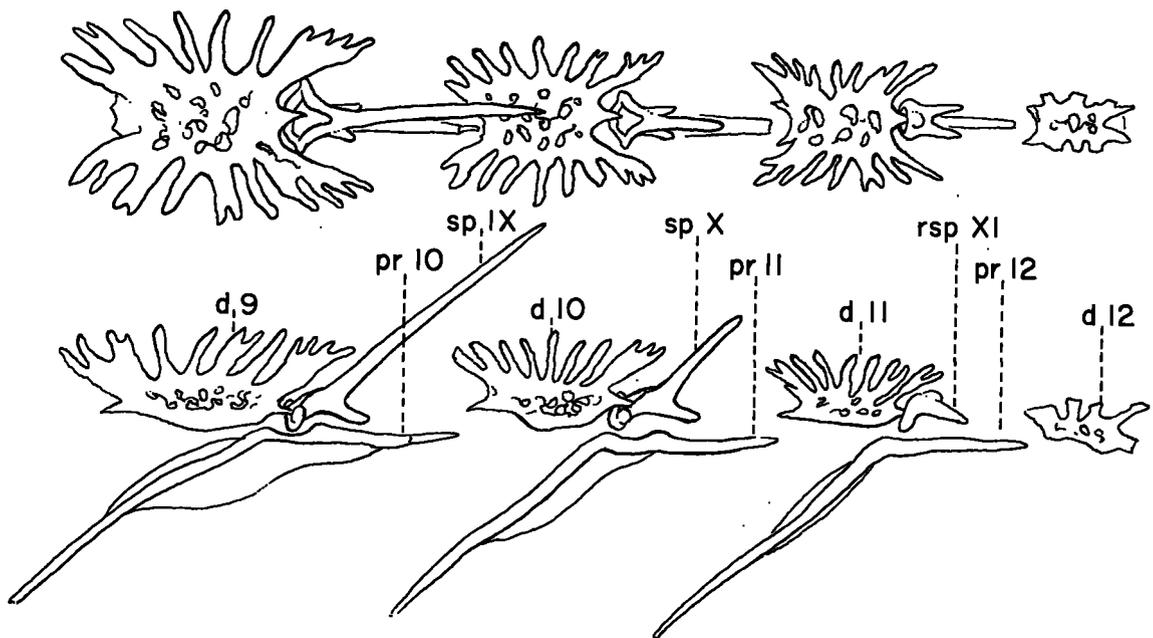


FIGURE 13.—Detailed dorsal and lateral views of the arrangement of the 9th and 10th spines and their interneurals in the first dorsal fin in the Pacific mackerel (also the rudimentary 11th spine): from a specimen 66.6 mm. long (see figs. 11 and 14). *d* 9 through 12, distal sections of the 9th through 12th interneurals; *pr* 10 through 12, proximal sections of the 10th through 12th interneurals; *rsp* XI, rudimentary 11th spine; *sp* IX and X, 9th and 10th spines.

Beginning anteriorly, the proximal section of each finlet interneural is bent almost at a right angle about half-way along its length. Its upper half is almost horizontal and parallel to the dorsal surface of the body, and the lower half is ventrally directed to terminate behind a neural spine, about one-third of the distance from the dorsal surface to the vertebral column. Counting posteriorly, this bend in the proximal section becomes less acute and closer to its innermost tip. As the angles of the proximal sections become more obtuse, the sections approach a horizontal position until the proximal section of the 6th finlet is almost parallel to the dorsal surface of the body. The inner tip of this last proximal section is bent to terminate behind the 25th neural spine (fig. 11). The distal section of each of the first 5 finlet interneurals is a long narrow bone, blunt at each end, and about equal in length to its proximal section. Each distal section lies almost horizontal in the body. The distal section of the interneural of the 6th finlet is divided into two parts. The innermost of these is short and stubby, about one-fourth the length of the proximal section, and lies forward of the base of the finlet. Directly

under the base of the finlet is the other section, blunt at its anterior end and bifurcate to two ventrolateral points at its posterior end. One other ossification occurs to tie together the distal and proximal sections of the finlet interneurals. This is a separate, spinous projection, fused to the posterior ventral surface of each proximal section, which extends for a short distance ventral to the posterior end of each distal section. This spine is also present on the middle section of the interneural of the 6th finlet. It extends under the ventral surface of the most posterior section.

First dorsal fin interneurals and the dorsal slot.—Often defined and recorded in the taxonomy of the Scombridae is the fact that the dorsal fin is depressible into a slot or groove. This slot was also recorded for one of the Gempylidae, *Xenogramma carinatum* Waite by Hildebrand (1946) from a report by Nichols and Lamonte, published in 1943. Starks (1910), in his discussion of a mackerel from the Canary Islands that he called *Scomber japonica* Houttuyn, stated that the "base-osts,"⁸ one in front of each spine, of the first dorsal are expanded and so broad that they "form a

⁸ Term not accepted by Eaton (1945).

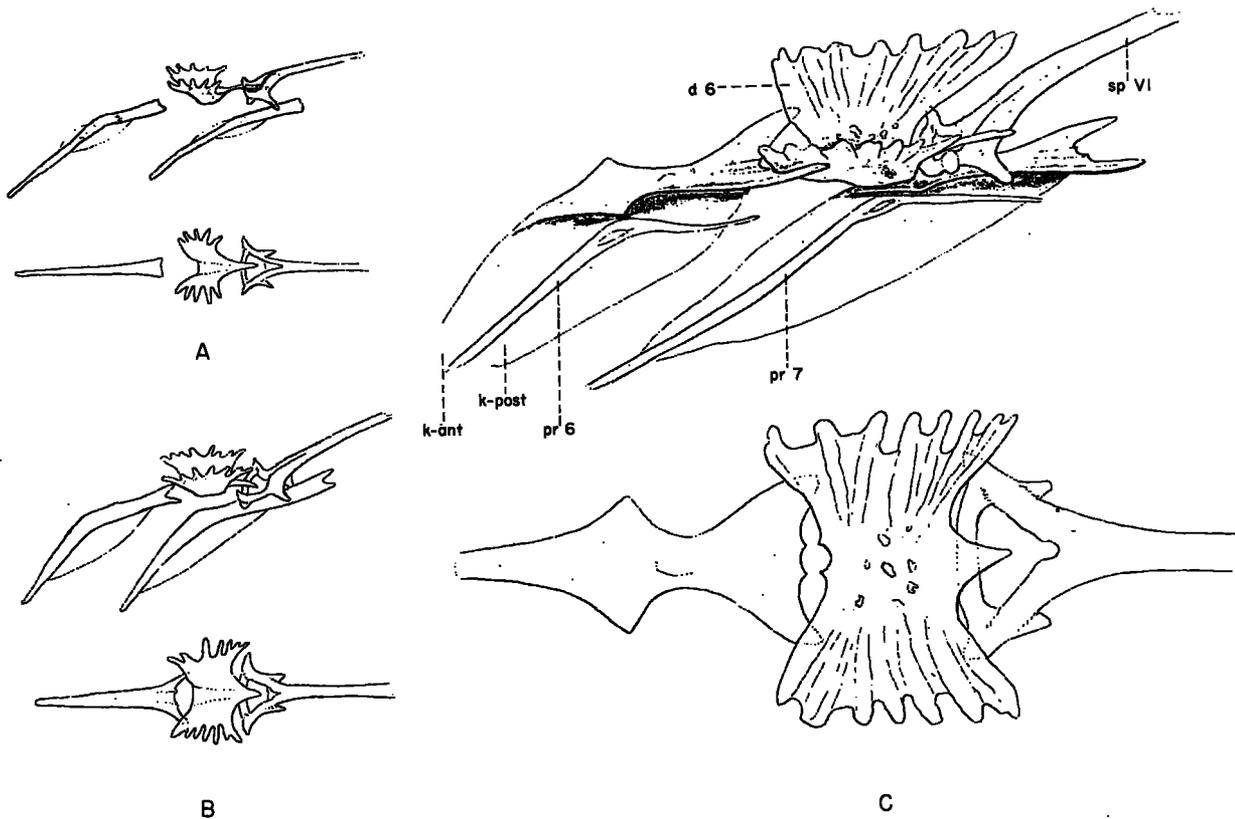


FIGURE 14.—Detailed dorsal and lateral views of the growth of the parts of the interneural of the sixth spine of the first dorsal fin in the Pacific mackerel, illustrating the formation of the dorsal slot (see figs. 11 and 12). *A*, from a specimen 26.4 mm. long. *B*, from a specimen 30.0 mm. long. *C*, from a specimen 66.6 mm. long. *d 6*, the distal section of the sixth spine; *k-ant*, anterior keel; *k-post*, posterior keel; *pr 6* and *7*, proximal sections of the sixth and seventh spines; *sp VI*, sixth spine. The proximal section of the seventh spine is omitted from each of the dorsal views in order to avoid confusion.

bony buckler that is visible under the skin of the undissected specimen."

The dorsal slot of the Pacific mackerel is one into which the dorsal fin is completely depressible. Its action, in and out of the slot, can be demonstrated even in preserved specimens. Observations made on live Pacific mackerel in aquaria showed that this first dorsal fin is used as a steering accessory. It is raised when rapid turns are executed and depressed when forward motion is resumed. This depression into a slot is probably an evolutionary advancement toward the further streamlining of the fusiform shape of the fast moving scombrids. Slower moving fishes with spinous dorsals are able to fold back, but not retract this fin. They do raise and lower it for steering, however, in much the same manner as does the Pacific mackerel.

Each interneural of the first dorsal fin, except

that of the first spine, is divided into two sections as are those of the finlets. However, wherein each section of each finlet interneural is a simple ossification with no modifications except for the connecting spines between the parts, the first dorsal fin interneurals are modified into complicated structures as illustrated in figure 13.

The interneural of the first spine is heavily keeled anteriorly and posteriorly. The keels decrease in width and length on the proximal sections of the interneurals posterior to the first one until there are none on those of the posterior section of the fin and the remainder of the distal sections posterior to and including that of the first spine of the second dorsal fin.

The palmate or alate modifications of the distal sections were first seen in the 24.6 mm. specimen (fig. 14A). They appear as small, stellate, lateral growths on each distal section between the bases

of the spines. Since the bases of the first two spines are crowded closely together, the distal section of the interneural of the second spine never grows very long, but remains a stubby, slightly broadened bone in that position. The distal section of the interneural of the third spine develops its alate structure but does not grow very long because of the proximity of the bases of the second and third spines. The longest of the distal sections is that of the interneural of the fourth spine, and its alate structures are correspondingly long. Counting posteriorly, and including the distal sections of the interneurals of the section of the first dorsal without spines, the lengths of the alate structures decrease in proportion to the lengths of the distal sections. Included in this series is the very small bone at the base of the spine of the first dorsal fin, which finally has no alate structures.

At first, the alate structures spread forward and laterally, and they become palmate with several anterior, lateral, and posterior projections on their outer edges (fig. 14B). Those from the one in front of the 10th spine to the one which precedes that of the 2d dorsal fin spine never spread very widely. Each of these distal sections forms a "Y" with its open ends the lateral edges of the palmate sections and its closed end the proximal section of the interneural. In the adult, the anterior, alate structures grow vertically outward and spread anteriorly and posteriorly. At this time, they very much resemble moose antlers. This upward trend of the alate structures decreases posteriorly until those at the posterior end of the fin remain in much the same flattened position of their earlier development. It is in this section that the slot becomes more shallow.

Before the lateral and vertical growth of the alate structures begins in the anterior section of the fin, the distal ends of the proximal sections become bifurcate into posterolateral spines which grow posteriorly to meet and interlock with the forward growing anterior edges of the alate structures of the distal sections. Toward the middle of the fin and posteriorly, this growth is not so well marked but still can be seen even in the sections associated with the sixth spine (fig. 14C).

In *Auaxis* species the alate structures are in the same positions on the distal sections of the interneurals as those of the Pacific mackerel. How-

ever, their greatest growth is lateral rather than anterior and posterior, with their consequent earlier lateral elongation into the moose-antler shape in specimens only 28 mm. in length. To make up for the anteroposterior form of growth in the Pacific mackerel, *Auaxis* also develops pronounced alate structures on the lateral posterior bases of the proximal sections. The lateral growth of the dorsal surfaces of these proximal sections in the Pacific mackerel can be seen beginning in 30.0 mm. specimens and becoming well developed in the 66.6 mm. specimen (fig. 14B and C). This does not grow vertically as it does in *Auaxis*.

Vertebral column

The vertebral column of the Pacific mackerel has a total of 31 vertebrae, 14 abdominal, and 17 caudal. Roedel (1952) reported that of counts made on 2,352 fish, only 10 specimens had other than 31 vertebrae, and these had either 30 or 32. The last vertebra, the urostyle, is discussed later. The terms, ultimate, penultimate, and antepenultimate, are given to the 30th, 29th, and 28th vertebrae, respectively. Haemal processes do not begin to develop in the Pacific mackerel until the larva is about 8.5 mm. in length. Until that time, the last of the abdominal and the first of the caudal vertebrae cannot be distinguished or counted as such. Eighty-two specimens longer than 8.5 mm. in length were examined. All of these except one had a count of 14 abdominal and 17 caudal vertebrae. The one different specimen, 16.8 mm. in length, had its first haemal spine developed on the 14th vertebra, thus having a count of 13 abdominal and 18 caudal vertebrae.

The process and order of development in the vertebral column is illustrated by a series of schematic drawings in figures 15a to f and 16a to d. Representations of the hypural and epural elements associated with the urostyle are also presented. The position of the abdominal vertebrae above the body midline is a consequence of the shape of the body cavity which lies ventral to the midline.

The vertebral counts, listed in table 3, were begun with the ossification of any part of a vertebral structure. In the Pacific mackerel, the first part or parts to develop in any vertebra, except the urostyle, are the neural and haemal processes.

The development of the vertebral column begins at about 6.0 mm. with the formation of the first three neuropophyses (fig. 15a). More of these develop posteriorly as the larva increases in length. At about 6.5 mm., the haemapophyses of the 15th through the 22d vertebrae appear (fig. 15b). After this, the development of the neural and haemal processes is very rapid. By the time the larva is about 10.0 mm. in length, all of these processes are developed except the 30th neural, which appears as a reduced structure at about 11.0 mm. (fig. 15c-f; fig. 16g and h).

Development of the vertebral centra.—The centra of the anteriormost vertebrae are the first to form and differentiate; then ossification proceeds slowly posteriorly. The 29th vertebra begins to develop before the 6th is complete (fig. 15f). The former is complete and the 28th developing dorsally and ventrally by the time the ventral section of the 30th vertebra begins (fig. 16a). The 30th vertebra develops so rapidly that it is complete before the 28th, which started before it, has joined its dorsal and ventral sections (fig. 16b). All of the others develop their dorsal and ventral sections at about the same time (fig. 16a and b). The completion of the vertebrae is about equal from both the anterior and posterior groups. Moving toward the center from both ends of the column, the centra fuse and become complete at about the 15th vertebra at about 15.5 mm. (fig. 16d). This system of ossification of the vertebral column is partially illustrated in a larva of *Auwis* species described by Wade (1951). Each centrum begins its ossification with its ventral section, followed almost immediately by the development of the dorsal section (fig. 15b, 3d vertebra; 15f, 29th vertebra; fig. 16b, 30th vertebra).

Ossification of each centrum proceeds on its periphery from the dorsal and ventral sections to join at the midline (fig. 15b through fig. 16d). A centrum is considered to be complete with the disappearance of its line of fusion. This completion is true only insofar as concerns the periphery of the centrum. Inward ossification from the periphery to the center follows later. Ossification on the periphery of each centrum is anterior to posterior on the first 27 vertebrae. The last three vertebrae first ossify to the centers on their peripheries and then outward to their anterior and posterior ends (fig. 16a and b).

Vertebral lengths vary according to stages of development. Each vertebra grows progressively longer but not in the order of its position in the vertebral column, so as to maintain its length as greater or smaller than those preceding or following it. This is shown in the following list of selected lengths and vertebra numbers. No vertebra was measured unless it had completed its peripheral fusion.

Length (in mm.) of vertebrae in Pacific mackerel

Standard length (mm.)	Vertebra number										
	2	3	10	11	15	16	22	23	28	29	30
8.67	0.08	0.08									
10.30	.12	.12									
11.16	.25	.25							0.12	0.17	0.10
13.50	.24	.24							.17	.20	.17
17.15	.36	.36	0.32	0.32	0.32	0.32	0.31	0.31	.27	.31	.17
24.6	.44	.44	.58	.58	.58	.54	.54	.54	.48	.49	.34

The middle-section vertebrae outgrow the anterior ones, and the 28th vertebra, initially shorter than the 29th, finally attains the same size as that of the latter. In older fish, the constricted appearance of the middle sections of the vertebrae is evidence that their increase in length is accompanied by the peripheral enlargement of the ends of each centrum. The beginning of this type of growth can be seen in the ultimate and penultimate vertebrae, as illustrated for the 14.0 mm. larva (fig. 16d).

The urostyle, its associated bones and vertebrae.—The urostyle begins to ossify at about 6.5 mm., after the tip of the notochord turns dorsally. There are initially six hypural bones associated with the urostyle, three above and three below the midline of the caudal fin. The four hypurals adjacent to the midline fuse in pairs, during larval development. The other hypural above the midline is a small triangular-shaped bone. The lowermost hypural is long and narrow with a posteriorly directed spine near its base. They are all present by 9.5 mm. The order of ossification of these hypurals is illustrated in figure 15b-f. At about 11.0 mm., a neural process appears along the dorsal curvature of the urostyle. The anterior of the two epurals appears at about 11.0 mm. and the posterior at about 14.0 mm. The neural process of the ultimate vertebra is reduced. The haemal processes of the penultimate and ultimate vertebrae and the neural process of the

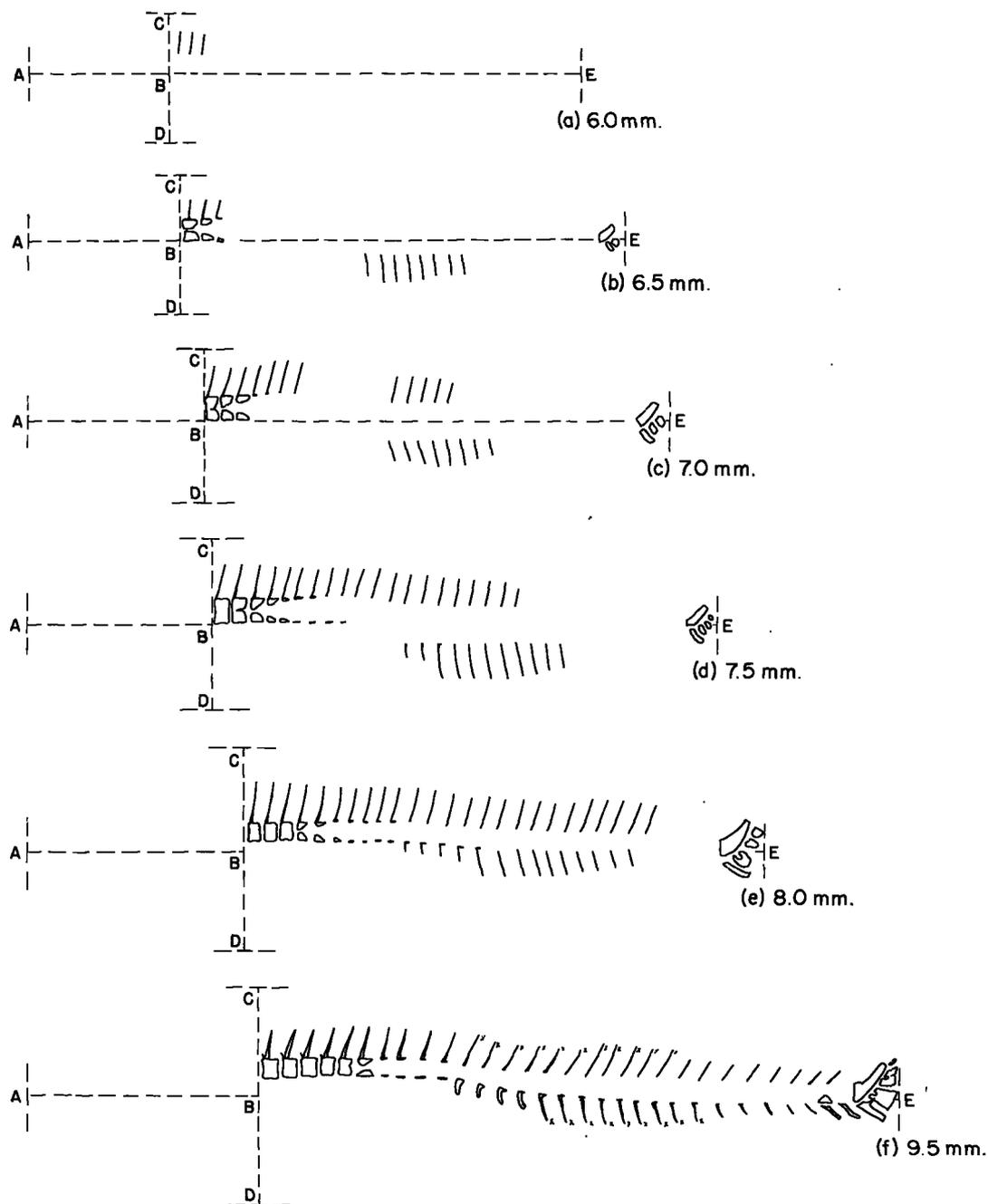


FIGURE 15.—Progressive ossification in the vertebral column in Pacific mackerel larvae from 6.0 to 9.5 mm. in length. The following are drawn to scale: A-B, head length; A-E, standard length; C-D, body depth. The x's on the neural and haemal processes in (f) denote fusion of these parts at their tips (see text).

penultimate vertebra are modified into truncate structures which aid in support of the secondary caudal rays. In the material studied, these processes were not directly connected to the vertebrae.

Formation of the vertebral arches and spines.—

In the early stages of their development, the neural and haemal processes are respectively based on the anterior-dorsal and anteroventral sections of their vertebrae. They grow dorsally and ventrally as the case may be, until they join at

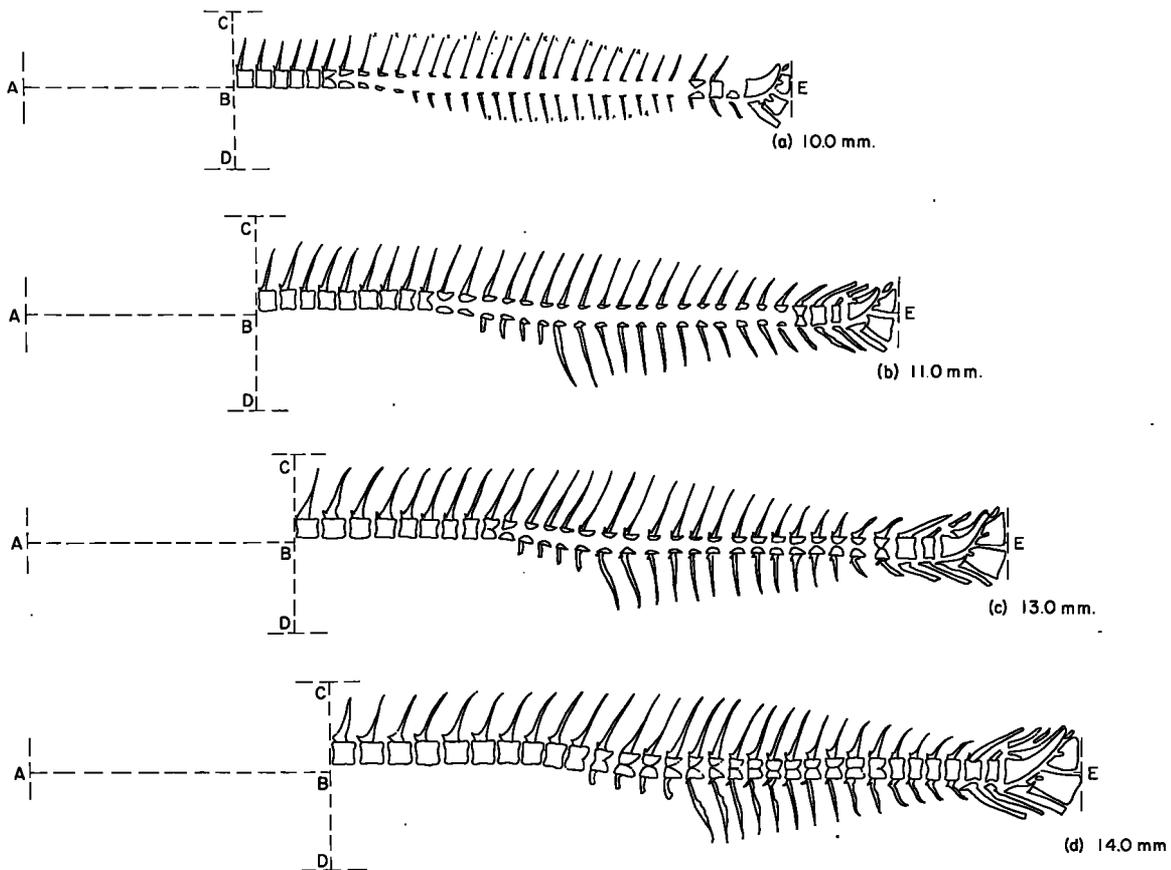


FIGURE 16.—Progressive ossification in the vertebral column in Pacific mackerel larvae from 10.0 to 14.0 mm. in length. The following are drawn to scale: *A-B*, head length; *A-E*, standard length; *C-D*, body depth. The *x*'s on the neural and haemal processes in (*a*) denote fusion of these parts at their tips (see text).

their tips to form the neural and haemal arches. Their sequence of ossification, fusion of their tips, and the ultimate formation of the spines are best referred to in the diagrams of figures 15 and 16. It can be seen that these sequences follow no single pattern or order for the same and associated parts. The vertebrae form (1) anterior to posterior (vertebrae 1 to 15), and (2) posterior to anterior (vertebrae 28 to 15). The neural processes form (1) anterior to posterior (vertebrae 1 to 7), and (2) middle to anterior and posterior (from vertebra 15 in both directions). The haemal processes form (1) anterior to posterior (vertebrae 15 to 30) and (2) posterior to anterior (vertebrae 14 to 11). Fusion at the tips of the neural processes occurs first in middle vertebrae and then proceeds in both directions while fusion of the tips of the haemal processes proceeds from anterior to posterior. The spines form almost immediately after the

fusion of the tips of their respective processes, and in the same order as that of the fusions.

At the beginning of their development, all of the neural and haemal processes are directed in a vertical, slightly posteriorward direction from the vertebral column. This relation is maintained in all of them throughout their growth, with the exception of those of the 26th through 30th vertebrae. The latter are the only processes not directly associated with the inner tips of the inter-spinal bones. The 26th, 27th, and 28th vertebral processes curve posteriorly until they lie almost parallel to the vertebral column. This occurs in the caudal peduncle, the section of least body depth. The angles formed by the modified and broad-ended processes of the penultimate and antepenultimate vertebrae are slightly less acute because of the increase in the depth of the body at the tail.

The lengths and directions of the neural and haemal spines vary according to their positions on the vertebral column. The neural spines in the anterior section are short and sometimes bend posteriorly at their tips as they approach the dorsal surface of the body. The only exception is the neural spine of the first vertebra, which is very short. On these vertebrae, the neuropophyses are the longest parts of the neural processes. The neural and haemal spines of vertebrae located in the middle and posterior sections follow the angles of their respective neuropophyses and haemopophyses. From the middle to the posterior sections of the vertebral column, the lengths of the spines increase as the lengths of the neuro- and haemopophyses decrease. These differences in the lengths of the sections of the vertebral processes result in the decrease in the size of the neural arches from the first to the ultimate vertebra, and in the decrease in size of the haemal arches from the 15th to the ultimate vertebra.

During all stages of development, the neural and haemal processes are based on the anterior ends of the vertebrae. As the vertebrae grow progressively longer, the neural processes seem to move posteriorly until they seem to be based on the centers of the vertebrae (fig. 15). This seeming movement is explained by the fact that each neural process is bent at such an angle that a point along its length, near its base, passes over the center of its respective vertebra. Posteriorward ossification of each vertebra is accompanied by additional ossification in the dorsal regions near the neural postzygopophyses. The dorsal ossification proceeds as far as that point on each neural process which is almost directly over the center of the vertebra. Thus, it finally appears as though each neural process had moved backward to become based on the center of each vertebra, or that each vertebra had grown beyond the base of the neural process. On the other hand, since there is no equivalent ventral ossification of the vertebrae, the haemal processes, except those in the caudal region, can be clearly defined as based on the anterior ends of the vertebrae throughout development. The ventral ossifications, analagous to the dorsal ossifications, take the form of haemal braces. No specimens were available for the study of this development in the sizes at which it takes place. In older fish, the

neural and haemal processes in the region of the caudal peduncle seem to originate from the posterior ends of the vertebrae. This is brought about by the posteriorward bending of the processes to allow for the narrow section of the caudal peduncle and the subsequent covering over of the processes by the peripheral growth of the vertebrae.

Ribs.—The ribs begin to ossify at about 10.0 mm. and are completed when the Pacific mackerel is about 15.0 mm. in length. There are 12 pairs of ribs in the Pacific mackerel and they are associated with all of the abdominal vertebrae except the first two. The attachment of the ribs to the vertebrae is on the lateral parapophyses (see discussion of their development below), and is progressively lower, laterally, starting with the first pair of ribs attached high on the anterolateral sections of the third vertebra. The ribs move off of the vertebrae onto the posterior sections of the parapophyses of the 9th vertebra and then a bit lower on the longer ones of the 10th vertebra. The succeeding pairs of ribs are attached to the ventral, posterior tips of the haemal arches of the 11th to 14th vertebrae. The ends of the haemal arches are flattened posteriorly to form points of articulation for the ribs. Ossification begins at the ends of the ribs for about one-third of their lengths and then proceeds inwardly to their bases on the vertebrae or haemal processes.

Epiplurals.—The last processes to form on the vertebrae are the epiplurals, sometimes called the intermuscular bones. Their formation begins at some time between 19 and 25 mm., starting on the first vertebra and finally reaching their full complement of 20 or 21 pairs at about 66.0 mm. These bones are based on the parapophyses in the anterior section of the column, and their projection into the lateral musculature is laterally perpendicular to the vertebral column. Beginning on the third vertebra, the bases of the epiplurals are always anterior to those of the ribs, and remain so until both move off the vertebrae onto the haemapophyses. They become widely separated from the ribs when the latter move onto the tips of the first haemal arch (on the 11th vertebra). Beginning with the 11th vertebra, the bases of the epiplurals are always located on the bases of the haemapophyses.

Zygapophyses.—In all fishes, the rigidity of the

vertebral column is maintained by the interlocking of the zygapophyses on the centra. These structures are formed as dorsal and ventral anterolateral and posterolateral projections on each centrum except as modified in certain sections of the column. In the Pacific mackerel, their formation begins at about 8.7 mm., and all of them are formed by the time the fish is about 14.0 mm. in length. This is only partially illustrated in figure 16. Ossification of the zygapophyses occurs before all of the centra have joined their dorsal and ventral sections. Modifications of the zygapophyses proceed with the further growth of the mackerel. In order to allow for lateral tail movement, the last five vertebrae and the urostyle are not interlocked. Articulation is either on the cartilagenous attachments of the vertebrae or on the haemal zygapophyses, the development of which is described below.

The neural zygapophyses appear first on the anterior vertebrae at about 8.7 mm. and then, at about 10.5-11.0 mm., on the vertebrae in the area between the anal and second dorsal fin. The order of formation is progressively posterior from the anterior center of ossification and in both directions from the posterior group. At first these projections are simple and spine-like, pointed anteriorly and posteriorly from their respective positions on the centra and the urostyle.

The posterior projections retain this simplified form, becoming more or less rounded on their posterior tips, from the 1st to the 23d vertebrae. The postzygapophyses on the 24th and 25th vertebrae become bifurcate. As development proceeds on the 26th to 29th vertebrae, the neural spines, progressively growing backward and bending parallel to the vertebrae, gradually envelope the postzygapophyses until they disappear entirely in the penultimate vertebrae. They are not covered on the ultimate vertebra.

The anterior, neural zygapophyses remain more or less unchanged on the 26th to the ultimate vertebrae. On the vertebrae anterior to these, each prezygapophysis grows anteriorly from its own vertebra to lie dorsolateral on the posterior section of the preceding vertebra and inside the postzygapophysis of that vertebra. As each prezygapophysis increases in length, it broadens and becomes antler-shaped. A projection appears just above its base and it is between this projection

and the main section that the posteriorward projection of the postzygapophysis of the preceding vertebra finally lies.

In the adult Pacific mackerel, the antler-shaped neural prezygapophyses can be seen from the 9th to the 25th vertebrae (Clothier 1950). Anterior to the 9th vertebrae they disappear, having been laterally enveloped by an ossification over the dorsal surfaces of the first eight vertebrae. The time at which this ossification begins is unknown. Its formation is anterior to posterior, and its presence, near completion, was first seen in a 66 mm. specimen. Kishinouye (1923) describes this ossification as a division of the neural arch into two parts; the lower arch for the "spinal cord" and the upper arch for the "dorsal ligament." His cross-section diagrams of the vertebrae of *P. japonicus* show that this arch extends to the 11th vertebra and is dorsally incomplete in the 13th. From the fact that the prezygapophyses can be seen on the 10th vertebra of his illustration and on the 9th in Clothier's drawing (1950) of *P. diego*, it is evident that the envelopment by this dorsal ossification is complete only to these vertebrae in each species and then continues between the dorsal zygapophyses of the vertebrae.

The anterior haemal zygapophyses first appear at about 11.0 mm. on the vertebrae in the area between the anal and second dorsal fins. Their order of formation and final form from the 15th to 27th vertebrae is the same as that of their neural counterparts in this section.

Anterior to the 15th vertebra, the haemal prezygapophyses appear as small anterolateral projections on the bases of the haemal arches. The most anterior of these small projections is on the haemal arch of the 12th vertebra.

The haemal postzygapophyses of the 28th vertebra may sometimes disappear into the bases of the haemal arches, as occurs to the neural postzygapophyses of the 29th vertebra. Ventral articulation of the ultimate and penultimate vertebrae is by means of anterior and posterior blunt, spinous projections which are the zygapophyses on the detached, modified haemal processes of these vertebrae. The only hypural having zygapophyses is the lowermost one. At about 8.5 mm., a single spine appears on each side of the base of this hypural, on its anterior dorsal sections. These spines grow posteriorly and laterally on both sides

of the ventral radial until they form two horizontal keels lateral to the anteroventral sections of the ventral hypural plate. The anterior, zygopophyses on this ventral radial appear at about 11.5 mm. and grow in much the same way as those on the haemal processes of the preceding vertebrae.

Parapophyses.—By definition, Clothier (1950) calls the processes of the haemal arches the haemapophyses, and names as parapophyses "the bony projections on each side of the anterior ends of the centra in the abdominal region to which the ribs are attached." I have already stated that in the Pacific mackerel the first pair of parapophyses to which the ribs are attached are those on the 9th vertebra. Anteriorly from this vertebra, the parapophyses "move up" onto the sides of the centra until the most anterior ones appear high and lateral on the first vertebra. Kishinouye's description of the haemal processes in *P. japonicus* (1923) implies that there are no parapophyses anterior to the haemal arches. He does not define the processes to which the ribs and epipleurals are attached other than to describe the positions of the latter on the anterior vertebrae. Since he worked only with adult fishes, he was not able to trace the development of these processes and see that the ridges present on the sides of the vertebrae are in reality the result of the parapophyses' being covered over by the peripheral ossification in the growth of the centra.

Ossification in other scombrid species

Comparisons of the rate of ossification in the Pacific mackerel with that in other scombrid species for this study have been limited to only two species of the latter. Those available to us were *Auris* species, the frigate mackerel, from 11.0 mm. and longer, and *Scomber scombrus*, the Atlantic mackerel, from 3.0 to 20.0 mm. in length.

Examples of differences in ossification in *Auris* species have been cited. The rate of ossification in this species is very much more rapid than that of the Pacific mackerel. The smallest specimen, 11.0 mm. in length, had already developed all of its vertebrae and fins at this early stage. The caudal keels showed their first scales at about 22 mm. In view of the more rapid rate of ossification in this fish, it is quite likely that its caudal keel development takes place much sooner than that of the Pacific mackerel, which time is un-

known. Herald (1951) points out the fact that different scombrid fishes seem to begin development of these structures at different times.

The Atlantic mackerel specimens did not stain very well, probably because the specimens were too old. However, what staining did take place seemed to show that the rate of development in this fish is about the same as that of the Pacific mackerel.

DISTRIBUTION AND ABUNDANCE OF LARVAE 1952-1956

The first information concerning the spawning areas of the Pacific mackerel was compiled from the survey cruises of the California Bureau of Marine Fisheries in 1936 through 1941 (Fry 1936b; Roedel 1949a.) These cruises were made chiefly inshore from Monterey, Calif., to Conception Bay in the Gulf of California, and included a few offshore exploratory lines west of Point Conception, the Channel Islands, San Diego, and to Guadalupe Island. The fact that offshore spawning was not delimited in those years is illustrated in Roedel's figure of the distribution of Pacific mackerel eggs and larvae in which both were taken at the offshore limit of the surveys. This has been further substantiated by extensive survey cruises of the California Cooperative Oceanic Fisheries Investigations in 1952-1956 (figs. 17-21).

Although these surveys have been conducted since 1949, the data are presented here only for the years 1952 through 1956. The more intensive, though less extensive coverage in these latter years has better served to clarify the abundance and distribution of Pacific mackerel larvae. The basic data for the distribution of the larvae for 1951 through 1956 have been given by Ahlstrom (1953, 1954b, 1958) and Ahlstrom and Kramer (1955, 1956, 1957). Survey cruises were made into the Gulf of California in 1956 and 1957 to determine the extent and abundance of Pacific sardine eggs and larvae in that area. In addition to data concerning the Pacific sardine, information was also gathered concerning the distribution of the eggs and larvae of many of the same fishes found on the Pacific coast. Of particular interest to this study, Pacific mackerel eggs and larvae were found to be present throughout the Gulf of California, as far north as Puerto Penasco.

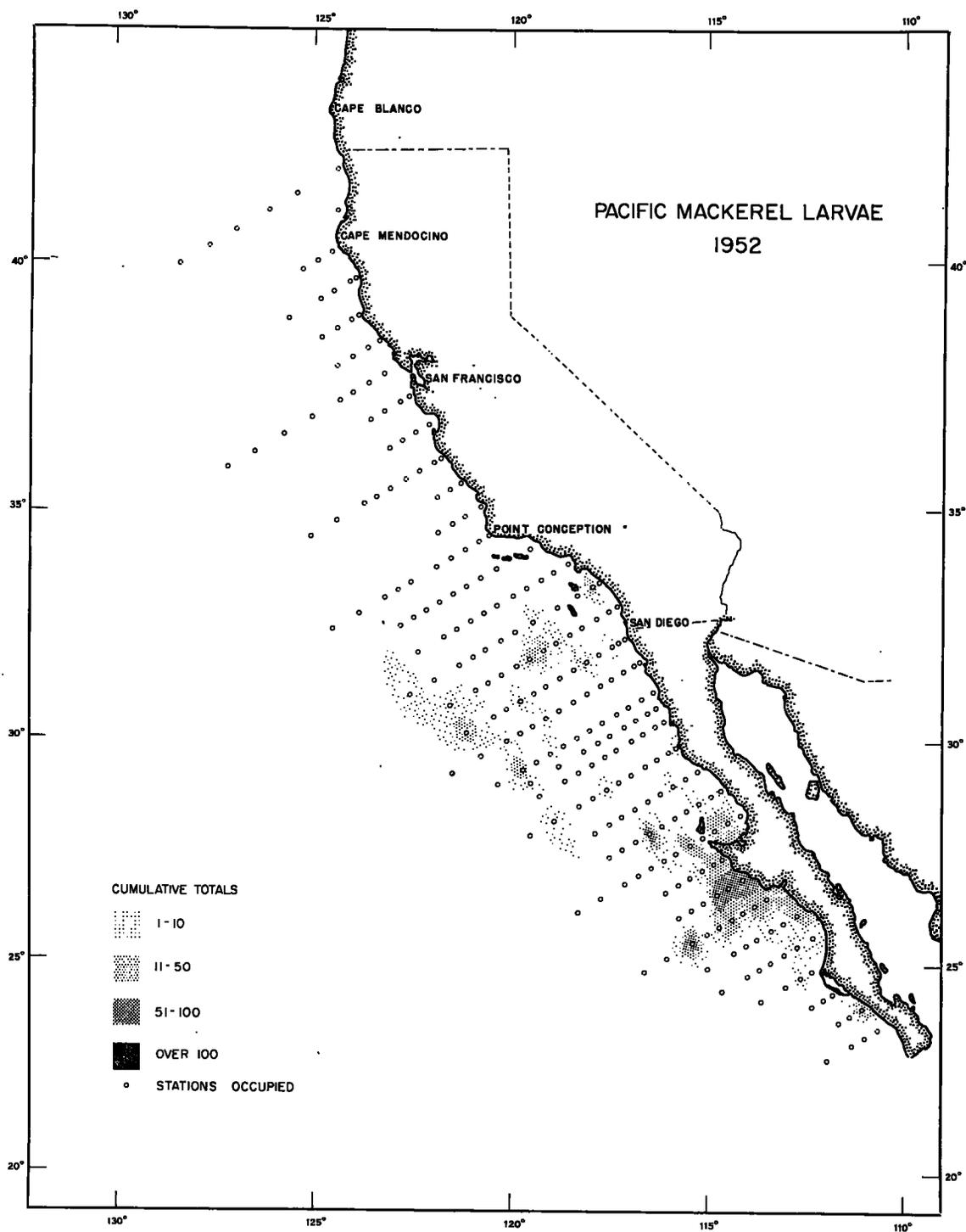


FIGURE 17.—Distribution and abundance of Pacific mackerel larvae in 1952. Cumulative totals represent the summation for the year of the standard haul totals of Pacific mackerel larvae taken at each station on each cruise.

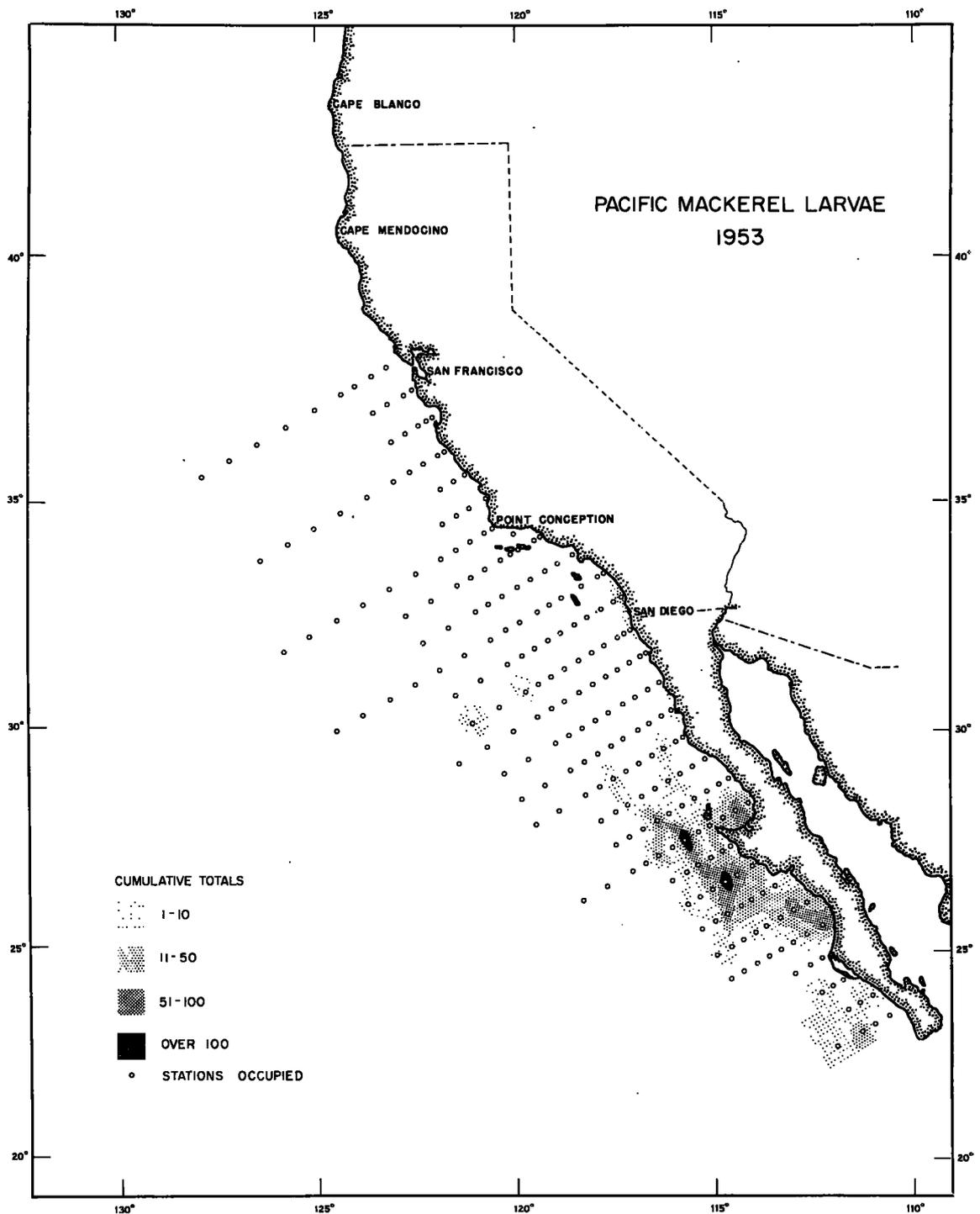


FIGURE 18.—Distribution and abundance of Pacific mackerel larvae in 1953. Cumulative totals represent the summation for the year of the standard haul totals of Pacific mackerel larvae taken at each station on each cruise.

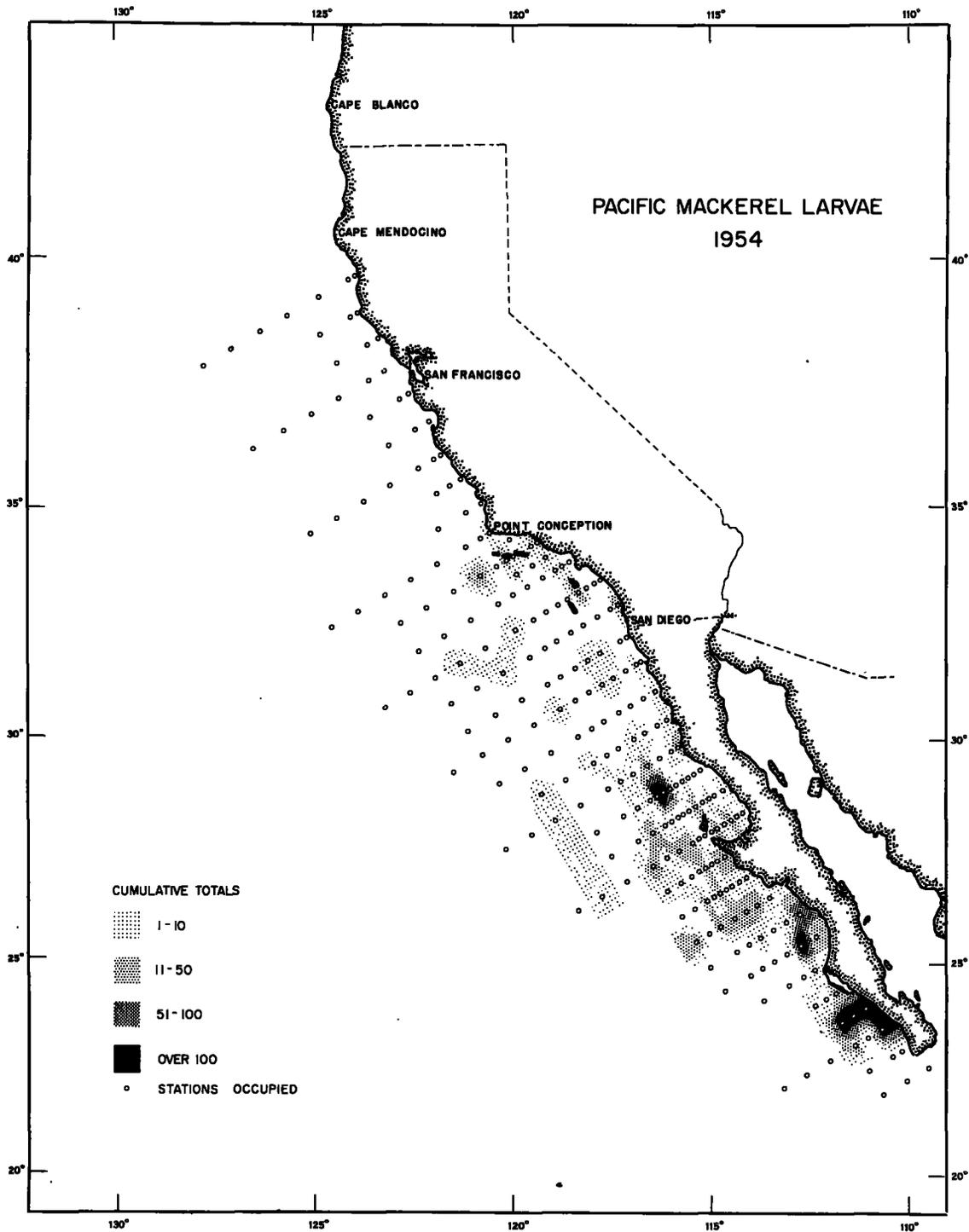


FIGURE 19.—Distribution and abundance of Pacific mackerel larvae in 1954. Cumulative totals represent the summation for the year of the standard haul totals of Pacific mackerel larvae taken at each station on each cruise.

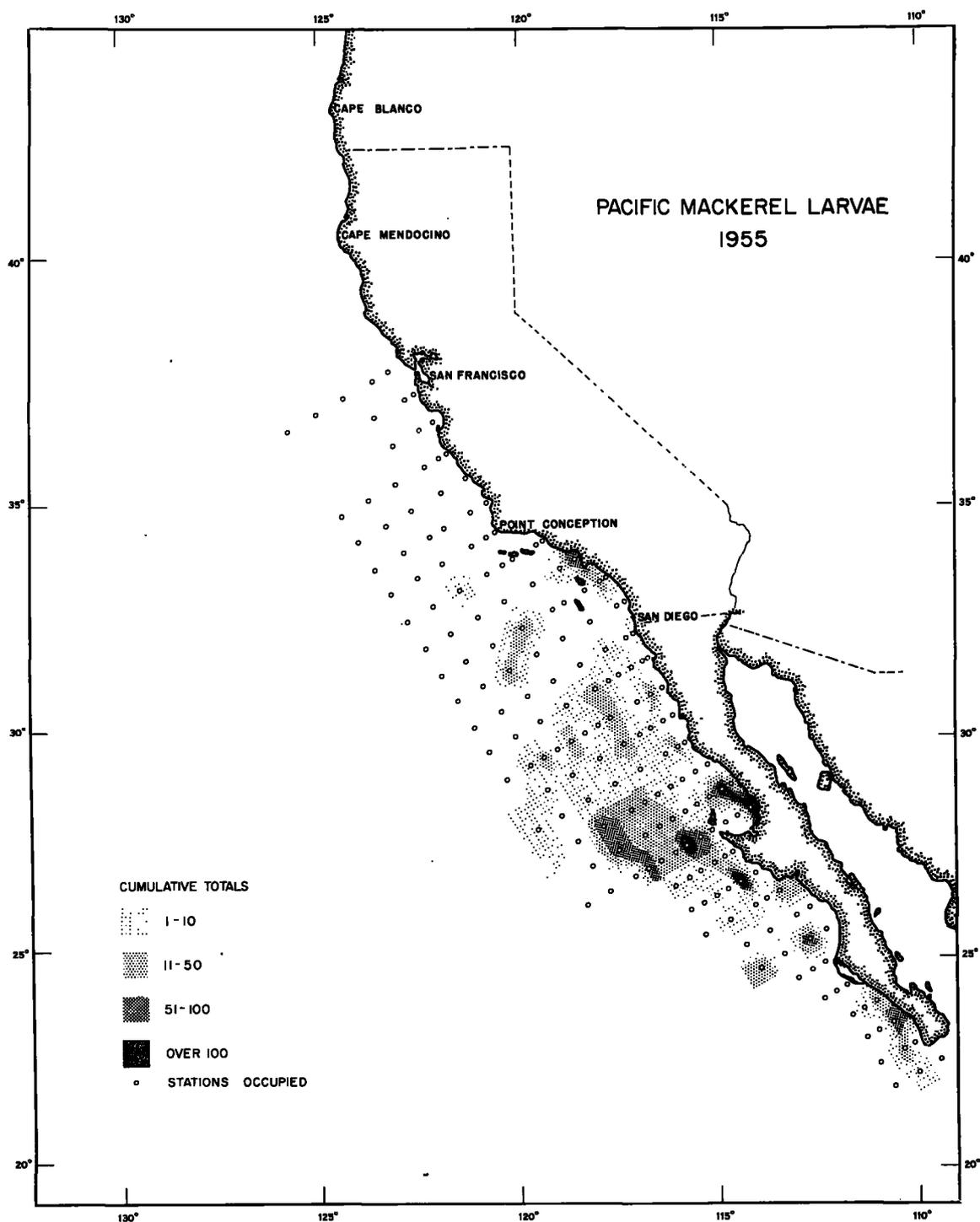


FIGURE 20.—Distribution and abundance of Pacific mackerel larvae in 1955. Cumulative totals represents the summation for the year of the standard haul totals of Pacific mackerel larvae taken at each station on each cruise.

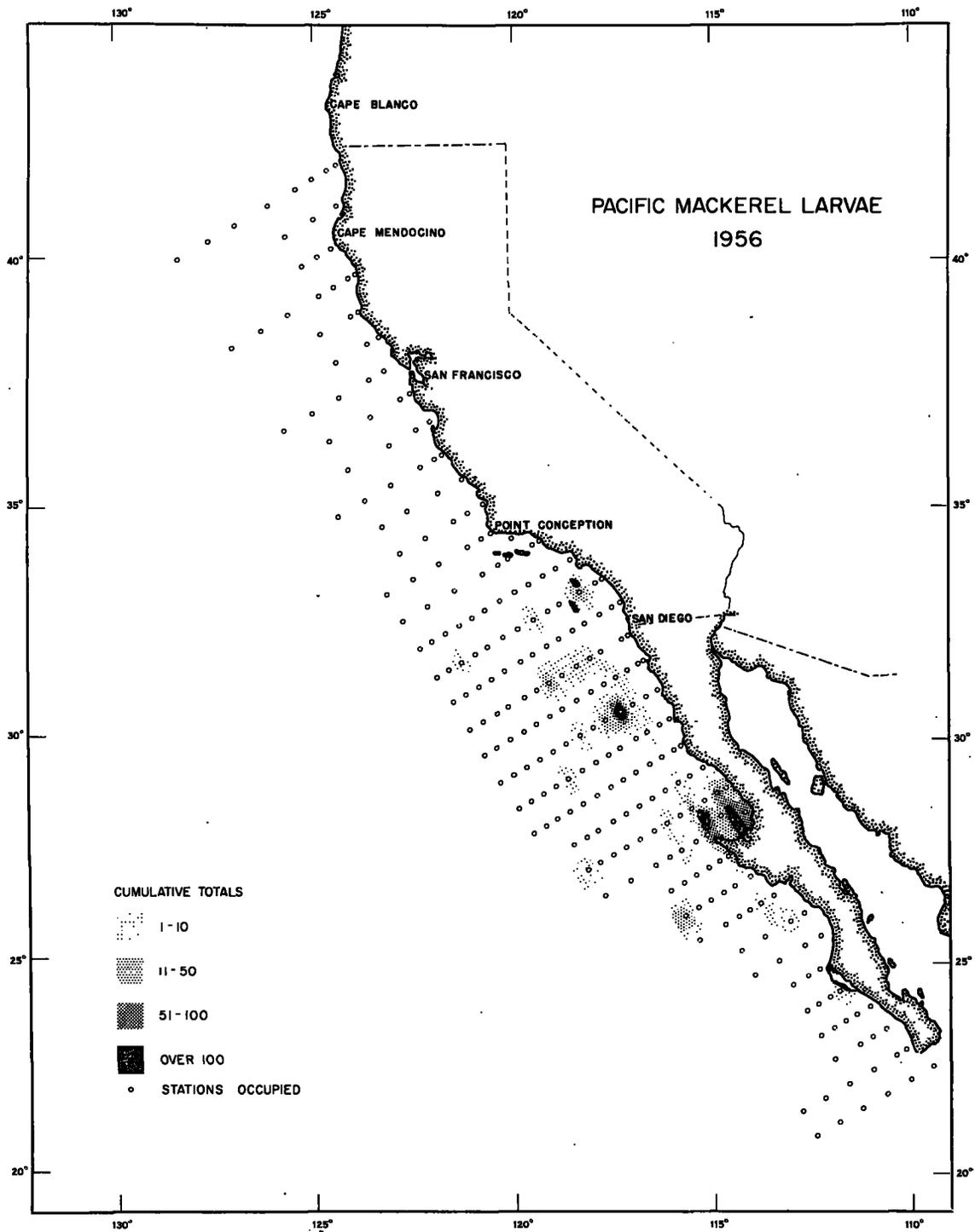


FIGURE 21.—Distribution and abundance of Pacific mackerel larvae in 1956. Cumulative totals represent the summation for the year of the standard haul totals of Pacific mackerel larvae taken at each station on each cruise.

CENSUS ESTIMATES

Monthly cruises on the Pacific coast were made by the California Cooperative Oceanic Fisheries Investigations in 1952 through 1956, except in the months and in the areas left blank in tables 8 and 10. The methods used to derive the census estimates of the abundance of Pacific mackerel larvae were the same as those used by Ahlstrom and Counts (1955). The sizes of the larvae are not taken into account, equal weight being given

to newly-hatched larvae and those approaching juvenile size. Although the rate of growth is unknown, complete larval development must extend over a period of more than one month, and it is possible, as in the case of the hake, that the same or parts of the same groups of Pacific mackerel in any given area were sampled more than once in consecutive cruises. The accuracy of these estimates is lower, therefore, by virtue of sampling only at monthly intervals.

TABLE 7.—Census estimates of the number of Pacific mackerel larvae in survey area during each cruise, 1952-56

[Estimates in billions.¹ Seven stations occupied north of line 60; two stations occupied north of line 80]

Lines	January	February	March	Late March	April	May	June	July	August	September	October	November	December	Total
1952														
60-77					0	0	0	0	0	0	0	0		0
80-93					4.9	0	3.4	19.2	0	0	0	0		27.5
97-107	0	0	0		0	4.1	21.8	8.2	0	0	0	0		34.1
110-120	0	0	0	0	1.6	17.3	17.3	6.8	8.0	0	9.7	2.4		63.1
123-137	2.0	0	8.8	10.9	57.5	25.4	0	0	5.0	27.7	5.3	0		142.6
140-157		10.8												10.8
Total	2.0	10.8	8.8	10.9	64.0	46.8	42.5	34.2	13.0	27.7	15.0	2.4		278.1
1953														
60-77					0	0	0	0	0					0
80-93					.1	0	3.1	0	0	0	0	0		3.2
97-107	0	0	0		0	0	4.0	.5	0		1.0			5.5
110-120	0	7.4	1.2	4.0	.7	14.0	67.3	4.4	58.8	3.3	9.6			170.7
123-137	.7	0	8.2	21.0	33.5	57.4	10.3	10.0	62.1		10.6			221.6
140-157	9.6													9.6
Total	10.3	7.4	9.4	25.0	34.3	71.4	84.7	14.9	120.9	3.3	21.2	0	7.8	410.6
1954														
60-77					0	0	0	0	0					0
80-93					0	1.1	10.6	22.4	0		0			34.1
97-107	0	0	0		0	3.6	7.3	5.1	1.0		0			17.0
110-120	0	0	.5		13.1	22.1	65.8	2.5	34.9		21.0			159.9
123-137	38.4	7.7	46.9		5.8	4.9	2.5	29.9	45.9		6.3			191.5
140-157	373.1													392.0
Total	411.5	7.7	47.4		18.9	31.7	86.2	59.9	81.8		27.3		22.1	794.5
1955														
60-77						0	0	0						0
80-93					0	0	15.9	23.9						39.8
97-107	0	0	0		39.4	10.1	4.4	0						53.9
110-120	0	0	18.4		170.2	4.0	126.9	23.8						343.3
123-137	0	0	46.7		1.7	9.6	42.5	6.3						106.8
140-157	54.9	3.5	.6											59.7
Total	54.9	3.5	65.7		211.3	23.7	189.7	54.0					.7	603.5
1956														
60-77					0	0	0	0						0
80-93					0	0	1.0	5.8						6.8
97-107	3.3	0	2.2		0	89.3	7.8	0	0		0			102.6
110-120	0	0	0		18.1	19.4	11.6	52.6	127.0	0	0			228.7
123-137	0	0	0		0	0	6.2	3.6	0	2.1				11.9
140-157	.6	0			0									.6
Total	3.9	0	2.2		18.1	108.7	26.6	62.0	127.0	2.1				350.6

¹ Data includes tenths of billions in order to save those values less than 1.0.² Survey cruise from line 40 south.

TABLE 8.—Census estimates of numbers of Pacific mackerel larvae by area, summarized from table 7

[Estimates in billions]

Area	Lines	1952		1953		1954		1955		1956	
		Number	Percent								
Central California	60-77	0	0	0	0	0	0	0	0	0	0
Southern California	80-93	27.5	9.89	3.2	0.78	34.1	4.29	39.8	6.59	6.8	1.94
Northern Baja California	97-107	34.1	12.26	5.5	1.34	17.0	2.14	53.9	8.93	102.6	29.26
Northern central Baja California	110-120	63.1	22.69	170.7	41.57	159.9	20.13	343.3	56.88	228.7	65.23
Southern central Baja California	123-137	142.6	51.28	221.6	53.97	191.5	24.10	106.8	17.70	11.9	3.39
Southern Baja California	140-157	10.8	3.88	9.6	2.34	392.0	49.34	59.7	9.89	.6	.17
Total		278.1	100.00	410.6	100.00	794.5	100.00	603.5	99.99	350.6	99.99

Areal occurrence

The monthly abundance of the Pacific mackerel listed by area in table 7 is summarized in table 8. No Pacific mackerel larvae have ever been taken north of Point Conception in any survey conducted by the California Bureau of Marine Fisheries or the California Cooperative Oceanic Fisheries Investigations. As determined by these cruises, the northernmost extent of the larvae is Point Conception and the southernmost is Cape San Lucas. The offshore extent of the Pacific mackerel populations is as far as 250 miles off northern Baja California and about 200 miles off central Baja California. The most westerly extent of the populations in these areas can be considered to be relatively unimportant as is shown by their offshore delimitation in 1952 through 1956 (fig. 17 through 21).

The greatest numbers of Pacific mackerel larvae are usually concentrated in the areas off upper central Baja California (lines 110-120) and lower central Baja California (lines 123-137). Because no surveys were made in these areas during two months in 1954, and four months in 1955, the estimated abundances for these areas in these years are too low by an unknown amount (Ahlstrom and Kramer, 1957).

In 1956, the abundance was greater off northern Baja California than in the preceding years. In 1952, approximately 22 percent of the larvae were taken off southern California and northern Baja California. In 1953, there was a sharp reduction in numbers in these areas to only about 2 percent of the total. In 1954 through 1956, the portions of the larvae taken off California and northern Baja California were 6.4, 15.5, and 31.2 percent

of the totals, respectively. Coverage in the area off southern Baja California (lines 140-157) was limited to a single cruise for several years, and did not exceed four cruises in any year. Even with such limited coverage, nearly 50 percent of Pacific mackerel larvae collected in 1954 were taken in this area. In contrast, only 0.2 percent of the total were obtained off southern Baja California in 1956.

Seasonal abundance

Fry (1936b) stated that Pacific mackerel spawning off southern California occurred from late April or early May to August, with the heaviest spawning from the middle of May to early July. These facts, derived from data collected in 1936, remain just about the same for the years 1952 through 1956. Table 9 is a summary of the monthly abundance of Pacific mackerel larvae over the whole of the survey area of the California Cooperative Oceanic Fisheries Investigations. Since Pacific mackerel spawning is sporadic; there is no definite seasonal peak for this fish, as is so well demonstrated by the larvae of jack mackerel (Ahlstrom and Ball, 1954) and hake (Ahlstrom and Counts, 1955). Instead, the seasons of abundance are made evident by grouping several months. Off southern California and northern Baja California most larvae are obtained between April through July (4 months), and off central Baja California between March through August (6 months). The presence of a large population in January 1954 (table 9) is due to a large concentration in southern Baja California (table 7). A plausible explanation for this sudden increase is the immigration into this area of a part of the adult spawning population from the Gulf of California.

TABLE 9.—*Census estimates of abundance of Pacific mackerel larvae by months, 1952-1956*

Month	[Estimates in billions]									
	1952		1953		1954		1955		1956	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
January.....	2.0	0.72	10.3	2.51	411.5	51.79	54.9	9.10	3.9	1.11
February.....	10.8	3.88	7.4	1.80	7.7	.97	3.5	.58	0	0
March.....	8.8	3.16	9.4	2.29	47.4	5.97	65.7	10.89	2.2	.63
Late March.....	10.9	3.92	25.0	6.09						
April.....	64.0	23.01	34.3	8.35	18.9	2.38	211.3	35.01	18.1	5.16
May.....	46.8	16.83	71.4	17.39	31.7	3.99	23.7	3.93	108.7	31.00
June.....	42.5	15.23	84.7	20.63	86.2	10.85	189.7	31.43	26.6	7.58
July.....	34.2	12.30	14.9	3.63	59.9	7.54	54.0	8.95	62.0	17.68
August.....	13.0	4.67	120.9	29.44	81.8	10.30			127.0	36.22
September.....	27.7	9.96	3.3	.80					2.1	.60
October.....	15.0	5.39	21.2	5.16	27.3	3.44				
November.....	2.4	.86								
December.....			7.8	1.90	22.1	2.78	.7	.12		
Total.....	278.1	99.98	410.6	99.99	794.5	100.01	603.5	100.01	350.6	99.98

VERTICAL DISTRIBUTION

Net tows for the vertical distribution of the eggs and larvae of the Pacific sardine and other fishes have been taken at various times between 1941 and 1955. Thus far, the vertical distribution of Pacific mackerel larvae and eggs is known from only three vertical series for the former and one of these three series for the latter (Ahlstrom 1959). Investigations of the vertical distribution of sardine eggs and larvae were conducted off southern California by the U. S. Fish and Wildlife Service in 1941 (Silliman 1943). Pacific mackerel larvae were obtained in two of the vertical series taken at locations now numbered by the California Cooperative Oceanic Fisheries Investigations as stations 92.39 and 94.47. Although vertical distribution series were taken at a number of localities during 1952-55, Pacific mackerel eggs and larvae were obtained only in a night series taken at station 120.50 in April 1955.

It has been previously stated that the areal distribution of Pacific mackerel larvae is similar to that of Pacific sardine larvae. The same can be said for their vertical distributions. Most sardine larvae (approximately 80 percent) are found in the upper 50 meters, with none being found deeper than 88 meters (Ahlstrom 1959). More than 99 percent of the Pacific mackerel larvae were taken above 50 meters, and over 80 percent above 23 meters. No larvae were collected below 66 meters.

Eggs found at the one station showed that they are less restricted in depth distribution than the larvae, some eggs occurring as deep as approximately 176 meters. Most eggs were taken between the surface and approximately 23 meters deep with abundance falling off sharply below this level (Ahlstrom, *ibid.*).

OCCURRENCE IN RELATION TO TEMPERATURE

At present, the depth distribution of Pacific mackerel larvae in relation to temperature can be based only on the vertical series data presented by Ahlstrom (1959). The temperature range in the depths at which these larvae were found in the three series varied from 14.1° to 17.1° C. Each series showed a variation in temperature of less than two degrees from the surface to the greatest depth at which larvae were found.

Temperature observations made on the California Cooperative Oceanic Fisheries Investigations surveys are more than adequate to encompass

the depth distribution of Pacific mackerel eggs and larvae. These were ascertained either from the data of reversing thermometers, usually spaced at 0, 10, 25, 50, and more meters in depth, or by bathythermograph records made to the bottom in shallow waters or to 137 or 274 meters in deep areas. The latter two depend on the bathythermograph range previously determined by station depth.

Ahlstrom and Counts (1955) observed that it is often desirable to express the temperature at any station as a single value, either as an average of the depth zone at which most of a certain type of larvae occur, or as a single temperature at a selected depth; that depth being the one at which the greatest concentrations of larvae are found. The choice of a depth which is representative of the vertical distribution of Pacific mackerel larvae is not a difficult one, as the greatest concentrations of larvae were obtained in the upper 20 meters. The 10-meter level was selected to be representative. The abundance of Pacific mackerel larvae in relation to the temperature at the 10-meter level is shown in table 10 and figure 22.

In 1952 through 1956, Pacific mackerel larvae were collected within a 16.5-degree temperature range, 10.3°-26.8° C. More than 68 percent of all occurrences, however, were found at temperatures between 14.0°-17.9° C, and approximately 94 percent of hauls containing larvae were taken at temperatures between 14.0°-21.9° C. The temperatures at which Pacific mackerel larvae were obtained in vertical distribution series were between 14.1°-17.1° C. The 13 larger hauls of Pa-

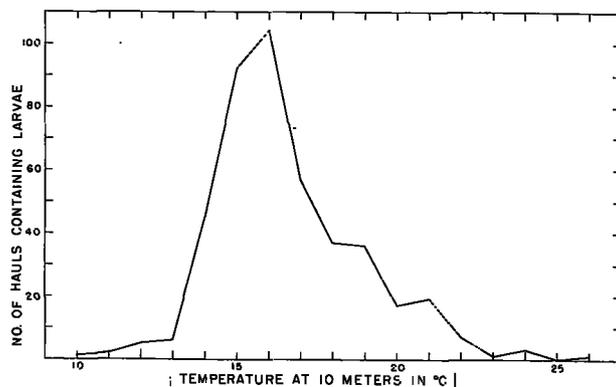


FIGURE 22.—Relation between water temperatures (at 10 meters) and number of hauls containing Pacific mackerel larvae, 1952 through 1956 (see table 10).

cific mackerel larvae (100 or more per haul) were taken at temperatures between 14.5°–21.6° C, with 7 of the hauls (table 11) falling within the temperature range of the vertical series. Only one of the larger hauls was taken off northern Baja California, nine off central Baja California, and three off southern Baja California.

TABLE 10.—Relation between water temperature (at 10 meters) and number of hauls containing Pacific mackerel larvae, 1952–56¹

Temperature at 10-meter level (° C)	Number of standard hauls that contained—					Total
	1–10 larvae	11–50 larvae	51–100 larvae	101–200 larvae	More than 200 larvae	
10.0–10.9	1	0	0	0	0	1
11.0–11.9	0	2	0	0	0	2
12.0–12.9	3	1	1	0	0	5
13.0–13.9	5	1	0	0	0	6
14.0–14.9	31	12	1	1	0	45
15.0–15.9	59	25	4	3	1	92
16.0–16.9	70	19	8	1	1	99
17.0–17.9	42	11	3	1	0	57
18.0–18.9	19	16	1	1	0	37
19.0–19.9	22	11	3	0	0	36
20.0–20.9	10	3	2	0	2	17
21.0–21.9	13	4	0	1	1	19
22.0–22.9	3	3	1	0	0	7
23.0–23.9	1	0	0	0	0	1
24.0–24.9	1	2	0	0	0	3
25.0–25.9	0	0	0	0	0	0
26.0–26.9	0	1	0	0	0	1
Total	280	111	24	8	5	428

¹ See figure 22.

TABLE 11.—Occurrences of 100 or more Pacific mackerel larvae, by area, at the 10-meter depth

Area	Station	Month	Year	Temperature °C	Number
Northern Baja California	103.45	May	1956	16.6	248
Northern central Baja California	113.45	June	1954	16.3	118
Do	113.47	do	1954	17.3	103
Do	117.30	do	1955	15.7	349
Do	118.35	August	1956	20.4	468
Do	118.39	July	1956	18.0	159
Do	120.50	April	1955	15.3	105
Do	120.50	June	1953	15.9	158
Southern central Baja California	127.40	March	1955	15.1	129
Do	127.45	May	1953	14.5	146
Southern Baja California	147.25	January	1954	21.0	462
Do	147.30	do	1954	21.6	150
Do	159.19	do	1954	20.2	361

¹ Occurrence within temperature range of vertical series (Ahlstrom, 1959)

SUMMARY

This is a detailed study of the embryonic and larval development of Pacific mackerel larvae. Also included is a discussion of the distribution and abundance of the Pacific mackerel larvae off the west coast of North America.

The Pacific mackerel egg is spherical, with a diameter ranging from 1.06–1.11 mm. It has a single oil globule (off center from the polar axis)

ranging in size from 0.22–0.31 mm., a very narrow perivitelline space, a clear yolk, and an unsculptured membrane.

Embryonic development is described for three stages: early (fertilization through closure of the blastopore); middle (blastopore closure to the tail twisting out of the embryonic axis); and late (tail twisting to hatching). Pigment begins to form after blastopore closure on the yolk near the pectoral region, and in a single line on the dorsum from head to tail. The pigment splits laterally to form two dorsal lines when the tail begins to grow away from the yolk. Just before hatching, the head becomes fairly heavily pigmented and the body pigment begins to migrate ventrally.

On hatching, the larva is approximately 3.0–3.5 mm. in length. The oil globule is located in the rear of the yolk-sac. Initial pigmentation after hatching is ventrally migratory on the body with some pigmentation on the head. Subsequent pigmentation is an increase in large, circular spots on top of the head, two elongated patches on the dorsal surface of the body, a vertical line of pigment on the base of the tail, a line of pigment on the posterior part of the lateral line, ventral pigment from the anus to the tail, and two or three spots on the ventral surface of the gut which disappear in late-stage larvae.

Size on size regressions of body parts on standard length could be adequately expressed as a straight line relation (fitted by least squares). The rate of increase of various body parts in relation to increase in standard length are as follows:

Head length	0.30 mm. per 1.0 mm. increase in standard length.
Distance snout to anus	0.69 mm. per 1.0 mm. increase in standard length.
Distance snout to 1st dorsal	0.36 mm. per 1.0 mm. increase in standard length.
Distance snout to 2d dorsal	0.66 mm. per 1.0 mm. increase in standard length.

The body depth in early stage larvae (to 10.7 mm. in length) increased at a rate twice that of the later stage larvae (10.7 to 18.9 mm. in length); the former at 0.27 mm. per 1.0 mm., and the latter at 0.15 mm. per 1.0 mm. increase in standard length.

In Pacific mackerel, the order of first appearance of the fins is as follows: larval pectorals

(without rays), caudal, pectorals (with rays), anal and second dorsal fins simultaneously, anal and dorsal finlets simultaneously, first dorsal, and ventrals. The development and appearance of the caudal keels is discussed in detail because of the occasional misconception that they are pseudo-fins with rays; each keel is made up of a series of scales assembled linearly on a complex curve. The ossification and formation of the vertebral column and its parts are discussed for centra, urostyle, hypurals and epurals, vertebral arches and spines, ribs, epipleurals, zygapophyses, and parapophyses. Development of the fin and finlet interspinal systems are described with particular emphasis on the individual parts of the interspinal bones; especially the continuity of the interneural system between the first and second dorsal fins and the complex structures forming the dorsal slot of the first dorsal fin.

Pacific mackerel larvae are distributed from Point Conception, California, south to Cape San Lucas, Baja California; offshore to a distance of 250 miles off northern Baja California and 200 miles off central Baja California; and throughout the Gulf of California. Larvae were mostly obtained during April through July off northern Baja California, and March through August off central Baja California. Data on the vertical distribution of eggs and larvae show that eggs occur from the surface to 176 meters deep, with the greatest concentrations between the surface and 23 meters deep; no larvae are found below approximately 66 meters, with about 99 percent above 50 meters and about 80 percent above 23 meters. Areal occurrences by temperatures were determined at the 10-meter level; all larvae were collected within a 16.5-degree temperature range (10.3–26.8° C); more than 68 percent occurred between 14.0° and 17.9° C, and 94 percent at temperatures between 14.0° and 21.9° C.

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APPENDIX

Measurements and meristic counts of all specimens (exclusive of juveniles and adults) of *Pneumatophorus diego* described

Standard length (mm.)	MORPHOMETRIC MEASUREMENTS (mm.)							MERISTIC COUNTS													
	Head	Eye	Depth	Snout to anus	Snout to 1st dorsal	Snout to 2d dorsal	Vertebrae†	Branchiostegal rays (left side)	Caudal fin		Pectoral fins		Second dorsal fin‡	Anal fin‡	Finlets		First dorsal fin	Ventral fin‡ (left side)			
									Principal	Secondary	Left	Right			D	V					
2.30	0.59	0.26	1	YS	1.07																
2.40		.26		YS	1.20																
2.45	.61	.26		YS	1.22																
2.45	.66	.26		YS	1.20																
2.55	.66	.28		YS	1.17																
2.58		.27		YS	1.22																
2.60	.69	.26		YS	1.25																
2.65	.66	.27		YS	1.16																
2.68	.61	.26		YS	1.25																
2.70	.54	.28		YS	1.02																
2.70	.69	.31		YS	1.17																
2.70	.66	.26		YS	1.25																
2.73	.66	.33		YS	1.02																
2.75	.61	.28		YS	1.25																
2.75		.31		YS	1.28																
2.75	.61	.38		YS	1.25																
2.78	.71	.28		YS	1.15																
2.86	.66	.28		YS	1.12																
2.88	.59	.33		YS	1.02																
2.91	.66	.36		YS	1.33																
2.91	.60	.32		YS	1.26																
2.91	.59	.31		YS	1.02																
2.96	.76	.38		YS	1.43																
2.96	.69	.33		YS	1.20																
2.98	.69	.38		YS	1.22																
3.01	.76	.38		YS	1.43																
3.06	.76	.38		YS	1.53																
3.09	.71	.38		YS	1.45																
3.11	.71	.43		YS	1.40																
3.16	.79	.38		YS	1.43																
3.21	.82	.38		YS	1.53																
3.32	.76	.41		YS	1.43																
3.34	.76	.41		YS	1.43																
3.42	.79	.41		YS	1.58																
3.42	.79	.41		YS	1.61																
3.42	.81	.43		YS	1.58																
3.49	.71	.46		YS	1.58																
3.57	.92	.43		YS	1.71																
3.72	.94	.43		YS	1.71																
4.03	.89	.44			.87																
4.13	1.02	.48			.97																
4.18	1.02	.51	1.05		1.89																
4.28	.92	.41	.82		1.78																
4.31	1.12	.54	1.15		2.19			2													
4.38	1.05	.51	1.10		2.12			1													
4.44	.99	.51	.99		2.09																
4.51	1.25	.64	1.15		2.30			4		4											
4.51	1.27	.64	1.35		2.55			4		4											
4.54	1.26	.59	1.22		2.35			3		4											
4.56	1.17	.56	1.10		2.30			1													
4.56	1.02	.60	.89		2.04																
4.62	1.22	.64	1.20		2.40			3		2											
4.62	1.02	.48	.79		1.94																
4.67	1.33	.64	1.33		2.50			4		8											
4.74	1.16	.54	1.20		2.30			2		2											
4.74	1.28	.64	1.28		2.45			4		4											
4.82	1.15	.51	1.17		2.24			2													
4.84	1.25	.54	1.15		2.30			1													
4.84	1.20	.54	1.17		2.30			1													
4.87	1.20	.59	1.25		2.37			2		4											
4.90	1.22	.51	1.07		2.07																
4.95	1.22	.57	1.17		2.37			4													
4.97	1.22	.56	1.33		2.55			2		2											
5.04	1.25	.61	1.33		2.65																
5.10	1.20	.54	1.15		2.37			1													
5.12	1.22	.54	1.07		2.30																
5.13	1.40	.69	1.48		2.65			5		8											
5.20	1.40	.64	1.43		2.52			3													
5.35	1.28	.54	1.22		2.42			1													
5.36	1.22	.54	1.20		2.55																
5.36	1.35	.64	1.33		2.60																
5.38	1.53	.64	1.45		2.96			5		10											
5.41	1.40	.61	1.35		2.70																
5.41	1.38	.61	1.39		2.75																
5.42	1.33	.59	1.35		2.52			2													
5.47	1.35	.71	1.35		2.62			5		9											
5.48	1.40	.64	1.38		2.68			3													
5.50	1.53	.69	1.53		2.98			5		11											
5.53	1.50	.71	1.53		3.04			5		11											
5.55	1.45	.61	1.40		2.75			5		7											
5.56	1.25	.56	1.10		2.35																
5.56	1.53	.69	1.50		2.93			4													
5.58	1.40	.61	1.35		2.80																
5.58	1.40	.64	1.28		2.70																
5.61	1.48	.69	1.45		2.86			4		9											

See footnotes at end of table.

Measurements and meristic counts of specimens (exclusive of juveniles and adults) of *Pneumatophorus diego*—Con.

MORPHOMETRIC MEASUREMENTS (mm.)

MERISTIC COUNTS

Stand- ard length mm.)	Head	Eye	Depth	Snout to anus	Snout to 1st dorsal	Snout to 2d dorsal	Verte- brae†	Branch- io- ste- gal rays (left side)	Caudal fin		Pectoral fins		Second dor- sal fin†	Anal fin†	Finlets		First dorsal fin	Ventral fin† (left side)	
									Prin- cipal	Secund- ary		Left			Right	D			V
										D	V								
5.61	1.58	0.71	1.50	2.93				4	12			LP							
5.64	1.73	.71	1.58	3.08				5	15			LP							
5.66	1.53	.71	1.53	3.09				5				LP							
5.68	1.50	.69	1.38	2.80								LP							
5.71	1.40	.64	1.30	2.68								LP							
5.74	1.61	.69	1.53	2.93				5	15			LP							
5.74	1.53	.66	1.48	2.65				5	12			LP							
5.76	1.38	.67	1.38	2.55								LP							
5.79	1.45	.66	1.48	2.86				3				LP							
5.81	1.45	.69	1.35	2.75								LP							
5.82	1.45	.66	1.50	2.83								LP							
5.83	1.68	.76	1.68	3.41				5	16			LP							
5.86	1.71	.69	1.66	3.14				5	12			LP							
5.86	1.43	.64	1.45	2.80								LP							
5.89	1.56	.66	1.40	2.96								LP							
5.90	1.53	.71	1.53	3.06				5	11			LP							
5.92	1.53	.69	1.43	3.04				5	11			LP							
5.94	1.56	.66	1.40	2.98				4	10			LP							
5.94	1.53	.71	1.48	3.11				5	9			LP							
5.94	1.65	.74	1.63	3.44				5	13			LP							
5.99	1.53	.69	1.58	3.08				4	10			LP							
6.03	1.63	.64	1.53	2.53			3					LP							
6.03	1.81	.79	1.78	3.51				5	16			LP							
6.04	1.46	.61	1.28	2.52								LP							
6.04	1.73	.79	1.53	3.54				5	16			LP							
6.07	1.45	.66	1.40	2.86				4	6			LP							
6.09	1.76	.79	1.78	3.37				6	17			LP							
6.10	1.76	.74	1.66	3.32				6	17			LP							
6.12	1.76	.79	1.76	3.37			2	6	17			LP							
6.17	1.56	.71	1.61	3.09								LP							
6.20	1.59	.64	1.33	2.73								LP							
6.22	1.71	.76	1.61	3.37				5	14			LP							
6.22	1.45	.69	1.40	2.91								LP							
6.22	1.48	.74	1.61	2.96				4	10			LP							
6.22	1.53	.74	1.71	3.16				4	10			LP							
6.32	1.66	.76	1.56	3.34				5	8			LP							
6.32	1.56	.74	1.58	3.14				4				LP							
6.34	1.53	.66	1.43	2.91								LP							
6.37	2.08	.84	1.88	3.90				6	17			LP							
6.38	1.63	.74	1.71	3.02				6	15			LP							
6.42	1.73	.72	1.67	3.11				3	8			LP							
6.45	1.58	.74	1.68	3.64				5	16		1	LP							
6.45	1.66	.79	1.68	3.39				4	6		1	LP							
6.46	1.97	.76	1.77	3.68			14	6	17		1	LP							
6.47	1.98	.89	2.04	3.95				6	17			LP							
6.55	1.68	.76	1.68	3.32				5	6			LP							
6.57	1.68	.84	1.73	3.95				6	17			LP							
6.58	1.66	.76	1.76	3.65				6	13			LP							
6.58	1.56	.74	1.66	3.34								LP							
6.60	1.68	.87	1.63	3.42				4	12			LP							
6.60	1.81	.82	1.73	3.75					13			LP							
6.62	1.68	.74	1.68	3.29								LP							
6.62	1.98	.84	1.78	3.95			23	6	15			LP							
6.62	1.94	.92	1.81	3.82					17		5	5							
6.66	1.81	.76	1.68	3.49															
6.66	1.53	.66	1.50	3.19															
6.68	1.76	.76	1.68	3.52															
6.68	1.84	.82	1.84	3.57				5											
6.71	1.99	.87	1.96	3.65			15	6	17		1	5	5						
6.72	1.58	.66	1.40	3.03															
6.76	1.94	.82	1.78	3.52				6	15										
6.76	1.86	.82	1.66	3.75			6	6											
6.78	1.86	.84	1.89	3.85				6	17		1								
6.81	1.81	.87	1.78	3.77				5	13										
6.83	1.76	.74	1.76	3.39				4	10										
6.86	1.66	.71	1.55	3.34															
6.94	1.84	.79	1.76	3.54				5	12										
6.96	1.78	.79	1.71	3.57															
7.02	1.98	.84	1.91	3.66				5	16										
7.04	1.84	.82	1.76	3.49															
7.06	2.09	.82	1.81	3.85			7	6	16										
7.06	1.86	.82	1.76	3.88															
7.06	1.78	.82	1.86	3.82				5											
7.09	1.73	.76	1.66	3.39				5	10										
7.11	1.91	.92	1.91	3.88			5	6	17		4	4							
7.14	1.86	.89	1.86	3.92				6	17		2								
7.19	2.12	.76	2.04	4.21			18	6	17		4								
7.19	1.86	.82	1.75	3.88															
7.19	1.89	.87	1.91	3.77			7	6	17		1	4							
7.24	2.01	.92	1.99	4.00			10	6	17			4	4						
7.32	1.91	.82	1.78	3.88				5	17										
7.34	2.09	.89	1.94	4.16			16	6	17		1	5							
7.37	1.94	.84	1.84	4.08					14										
7.37	2.07	.74	2.04	4.00			16	6	17		1	4							

See footnotes at end of table.

Measurements and meristic counts of specimens (exclusive of juveniles and adults) of *Pneumatophorus diego**—Con.

MORPHOMETRIC MEASUREMENTS (mm.)

MERISTIC COUNTS

Standard length (mm.)	Head	Eye	Depth	Snout to anus	Snout to 1st dorsal	Snout to 2d dorsal	Vertebrae†	Branchiostegal rays (left side)	Caudal fin		Pectoral fins		Second dorsal fin	Anal fin‡	Finlets		First dorsal fin	Ventral fin (left side)		
									Principal	Secondary	Left	Right			D	V			D	V
7.39	2.01	0.79	1.84	3.95				6	16											
7.40	2.01	.82	1.78	3.90				6	16											
7.47	2.12	.89	2.09	4.39			24	6	17		1	4								
7.47	1.94	.84	1.94	3.95				6	17											
7.56	2.02	.79	1.89	3.85				4												
7.62	1.99	.84	1.86	3.88				6	16											
7.71	2.09	.82	1.81	3.85				4												
7.93	2.19	.94	2.07	4.67			24	7	17	2	2	7	7	6	10					
7.98	2.17	.94	2.14	4.56				6	17	1	1	6	6	6						
8.03	2.24	.97	2.32	4.59				26	17	2	2	6	6	6						
8.04	2.37	1.07	2.22	4.74				25	17	2	2	7	7	6						
8.05	2.50	1.02	2.17	4.90				25	17	2	2	6	6	7						
8.05	2.32	1.05	2.27	4.84				7	17	3	2	8		7						
8.13	2.04	.82	1.96	4.05																
8.15	2.37	1.10	2.30	4.74				7	17	2	2	7		8						
8.20	2.40	.94	2.24	4.64																
8.20	2.52	1.04	2.32	5.04			27	7	17	3	2	8								
8.21	2.09	.89	2.07	4.54										11		1				
8.24	2.04	.94	1.91	4.13				21	6	17		5	5							
8.24	2.17	.99	2.17	4.59				23	7	17		8	8							
8.25	2.27	.99	2.17	4.84				23	7	17	1	1								
8.30	2.37	.94	2.17	4.69				24	7	17	2	2	7							
8.35	2.67	1.05	2.22	4.84				31	7	17	3	3	8	9	11	4	3	IV		
8.45	2.77	1.09	2.37	5.09				28	6	17	1	2	7	7	8					
8.48	2.50	.99	2.30	5.04				31	7	17	1	2	9	9	I, 11	7	1			
8.67	2.47	1.07	2.22	4.92				31	7	17			9	9	I, 11	8	4	VI		
8.67	2.17	.92	2.19	4.69									9	9						
8.77	2.40	1.05	2.30	5.02									9	9						
8.89	2.72	1.19	2.42	5.63									8	8	I, 11	8	4	VI		
8.94	2.67	1.09	2.42	4.99			25	7	17	2	2	7	7	8						
9.03	2.40	1.02	2.22	4.82			23	7	17	2	2	5	6	7						
9.09	2.37	.99	2.32	4.89																
9.10	2.65	1.07	2.35	5.41			31	7	17	3	3	9	9	11	11	3	3			
9.38	2.52	1.05	2.30	5.48			31	7	17	3	3	8	8	10	11	1	1			
9.39	2.67	1.04	2.42	5.14			25	7	17	3	3	7	8	7						
9.40	2.65	1.10	2.47	5.25			27	7	17	3	3	8	9	9						
9.43	2.58	1.10	2.52	5.74								10	10	11	I, 11	1	1			
9.44	2.67	1.04	2.42	5.28			31	7	17	3	3	9	9	I, 11	10	1	1			
9.45	2.65	1.10	2.55	5.65			31	7	17	3	3	9	9	I, 11	10	1	1			
9.48	2.82	1.10	2.52	5.38			31	7	17	3	3	9	9	I, 11	10	1	1			
9.49	2.67	1.04	2.27	5.04			24	7	17	2	2	5	6	11	I, 11					
9.67	2.82	1.10	2.55	5.67			30	7	17	3	3	9	9	11	I, 11	1	1			
9.78	2.77	1.08	2.46	5.53										10						
10.03	2.92	1.14	2.52	6.93																
10.12	2.93	1.10	2.55	6.14			31	7	17	4	4	10	10	I, 11	I, 11	5	5	IV		
10.30	2.90	1.10	2.60	6.00			31	7	17	3	3	9	9	I, 11	I, 11	2	2			
10.45	2.80	1.15	2.65	6.30			31	7	17	3	3	9	8							
10.67	3.21	1.28	2.72	6.27			31	7	17	4	4	11	11	I, 11		5		IX		
10.70	3.00	1.07	2.75	6.50			31	7	17	4	4	10	10					2		
11.10	3.15	1.25	2.95	6.60			31	7	17	3	3	10	10					3		
11.15	3.20	1.22	2.80	7.20	4.05	7.20	31	7	17	4	4	11	12	11	I, 11	5	5	VI		
11.16	3.31	1.28	2.86	7.06	4.45	7.41	31	7	17	6	6	14	14	I, 11	I, 11	6½	6½	VIII		
11.45	3.45	1.30	2.90	7.10	4.45	7.40	31	7	17	5	5	12	13	I, 11	I, 11	6½	6½	VII		
11.71	3.26	1.23	2.88	7.16		7.16	31	7	17	4	4	11	11	I, 11	I, 11	5	5	VI		
11.76	3.26	1.24	2.72	7.01	4.35	7.61	31	7	17	5	5	10	10	I, 11	I, 11	5	5	VII		
12.70	3.75	1.48	3.20	7.90	4.80	8.25	31	7	17	7	7	15	15	I, 11	II, 11	6½	6½	X		
13.24	3.56	1.33	3.06	8.10	4.74	8.50														
13.24	3.95	1.53	3.21	8.10			31	7	17	6	8	14	14	I, 11	II, 11	6½	6½	VIII		
13.50	4.25	1.40	3.35	8.65	5.20	8.65	31	7	17	6	6	13	14	I, 11	II, 11	6½	6½	VIII		
13.73	3.75	1.43	3.21	8.30	5.19	9.04														
13.80	4.10	1.40	3.26	9.25	5.25	8.90	31	7	17	7	7	15	15	I, 11	II, 11	6½	6½	X		
14.27	4.45	1.43	3.46	9.62	5.78	9.83														
14.30	3.95	1.33	3.06	8.60	5.30	9.30	31	7	17	6	6	15	14	I, 11	II, 11	6½	6½	X		
14.60	4.15	1.45	3.80	9.30	5.70	9.60	31	7	17	7	7	15	15	I, 11	II, 11	6½	6½	X		
14.80	4.20	1.40	3.11	9.20	5.50	9.50	31	7	17	7	7	15	16	I, 11	II, 11	6½	6½	X		
15.00	4.35	1.46	3.26	9.30	5.70	9.80	31	7	17	7	7	16	15	I, 11	II, 11	6½	6½	X		
15.20	4.25	1.41	3.41	9.40	5.60		31	7	17	8	8	17	17		II, 11	6½	6½	X		
15.80	4.54	1.56	3.46	10.40	5.90	10.20														
15.90	4.66	1.58	3.53	10.10	6.20	10.60	31	7	17	8	8	17	18	I, 11	II, 11	6½	6½	X		
16.00	4.54	1.63	3.21	10.10	5.90	10.30	31	7	17	7	7	16	15	I, 11	II, 11	6½	6½	X		
16.60	4.40	1.56	3.56	10.40	6.20	10.80	31	7	17	8	8	17	17	I, 11	II, 11	5	5	X		
16.60	4.84	1.53	3.90	10.97	6.57	10.92														
16.75	5.15	1.70	3.70	10.55	6.45	10.83	31	7	17	9	9	17	18	I, 11	II, 11	6½	6½	IX		
16.80	4.99	1.68	3.72	10.70	6.30	11.00	31	7	17	8	8	17	18	I, 11	II, 11	6½	6½	X		
17.15	4.95	1.60	3.85	10.85	6.35	11.10	31	7	17	9	9	17	17	I, 11	II, 11	6½	6½	X		
17.20	5.00	1.63	3.90	11.00	6.45	11.30	31	7	17	9	9	17	18	I, 11	II, 11	6½	6½	X		
17.24	4.89	1.68	3.70	10.92	6.47	11.01														
18.90	5.50	1.71	4.00	12.60	6.80	12.40	31	7	17	9	9	17	18	I, 11	II, 11	6½	6½	X		

*See tables 2 and 3 for averages of size groups. Measurements and counts include all specimens described in this study.

†Vertebral counts are based on first appearance of any part of a vertebral process without differentiation of spines or vertebrae (see figs. 15 and 16).

‡Second dorsal, anal, and ventral fins: arabic numeral alone represents early development; no differentiation between spines and rays. When roman numerals are used for spine counts such spines are indicated as the basis of known adult counts although actual differentiation in early stages may not be apparent.

¹YS, yolk sac larvae.

²LB, larval bud.

³LP, larval pectoral.

⁴All vertebral counts after 6.4 mm. include the urostyle (see fig. 15).

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FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

BUREAU OF SPORT FISHERIES AND WILDLIFE, Daniel H. Janzen, *Director*

SYNOPSIS OF
STRIGEOIDEA (TREMATODA) OF FISHES
AND THEIR LIFE CYCLES

BY GLENN L. HOFFMAN



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ABSTRACT

This report is an aid to the identification of the strigeoid metacercaria found in the fishes of the world. It includes a condensed record of the known life cycles of those strigeoids that have fish as their second intermediate host. The parasites are placed in four metacercarial groups of strigeoids (*Tetracotyle*, *Diplostomulum*, *Neascus*, and *Prohemistomulum*), rather than grouped in the usual taxonomic fashion. The synopsis is world-wide, although keys are given only for the species of *Tetracotyle*, *Diplostomulum*, and *Neascus* of North America. Representatives of the different genera are figured and drawings are included of all available illustrations of strigeoid metacercariae of fishes.

SYNOPSIS OF STRIGEOIDEA (TREMATODA) OF FISHES AND THEIR LIFE CYCLES

By GLENN L. HOFFMAN, *Fishery Research Biologist*, BUREAU OF SPORT FISHERIES AND WILDLIFE

The object of this review is to bring together information concerning the life histories and identification of all of the known strigeoids (members of the superfamily Strigeoidea) which have fish as their second intermediate hosts. Dr. G. R. LaRue has suggested (personal communication) that the common name for this group should be "strigeoid" rather than "strigeid" because the latter might be confused with one family, Strigeidae, of the Strigeoidea. As used here, strigeoid refers to the entire superfamily, Strigeoidea Railliet 1919, which contains the families Strigeidae Railliet 1919, Diplostomatidae Poirier 1886, Cyathocotylidae Poche 1926, Proterodiplostomatidae Dubois 1937, Bolbocephalodidae Strand 1935, and Brauninidae Bosma 1931. In the examination of fish, whether for routine surveys, strigeoid life history studies, or in using the parasites for physiological, morphological, and pathological studies the immediate problem is the identification of the parasite. The larval strigeoids of the fish are often very difficult to identify and, in some instances, the species cannot be identified with certainty without rearing specimens to the adult stage in an experimental final host.

The following strigeoids have been reared to adult stage and identified:

In unfed chicks: *Posthodiplostomum minimum oen-trarchi* and *P. m. minimum* by Ferguson (1937), Hoffman (1958a); *Ornithodiplostomum ptychocheilus* by Hoffman (1954); *Diplostomum bacri eucaliae* by Hoffman and Hundley (1957); *Apatemon gracilis pellucidus* by Hoffman (1959); *Hysteromorpha triloba* by Hoffman (this paper); and *Liustovicella szidati* by Anderson and Cable (1950).

In domestic ducks: *Apatemon fuligulae* and *A. pellucidus* by Yamaguti (1933); *Diplostomum phoxini* by Arvy and Buttner (1954), Bell and Hopkins (1956), and Rees (1955); *Ornithodiplostomum ptychocheilus* by Van Haits-

ma (1930); *Cyathocotyle gravieri* (cf. Dubois, 1938); *C. melanittae* by Yamaguti (1942).

In gulls: *Cotylurus pileatus* (cf. Dubois, 1938); *Mesophorodiplostomum pricei* (cf. Dubois, 1938).

In herons: *Hysteromorpha triloba* adults and non-ovigerous adults; *Mesostephanus odhneri* (cf. Dubois, 1938).

In hawks: *Neodiplostomum perlatum* (cf. Dubois, 1938). In owls: *Diplostomum bacri eucaliae* by Hoffman and Hundley (1957).

In cats and dogs: *Mesostephanus appendiculatus*, *Prohemistomum vivax* (cf. Dubois, 1938); *Prosostephanus industrius* by Tang (1941).

In mice: *Paracoenogonimus ovatus* by Komiya (1938). In snakes: *Prohemistomum chandleri* by Vernberg (1952).

Posthodiplostomum minimum has been reared to adult stage in culture by Ferguson (1940); and *Diplostomum phoxini* has been reared by Bell and Smyth (1958). The keys by Dubois (1938, 1953) are very useful in identifying the adults.

Only one strigeoid, a cyathocotylid (*Holostephanus ictuluri*) has been recorded as an adult from fish; and only one strigeoid metacercaria, again a cyathocotylid (*Szidatia joyeuxii*) has been recorded from frogs as well as fish.

Briefly, the following routine may be used for examining fish for strigeoid metacercariae:

(1) *Skin*.—If cysts are pigmented (usually with melanin, black, or sometimes xanthine, yellow), the presence of the cysts, about 1 mm. in diameter, is obvious; if not pigmented they are often discerned by their slightly raised surfaces. The fins should be examined in a physiological salt solution under the dissection microscope.

(2) *Muscle*.—If pigmented, the cysts are easily discovered as the tissue is teased apart in the saline solution; a section is examined under the dissection microscope as the muscle is teased apart.

(3) *Gills, gill arches, and viscera*.—Examine under dissection microscope.

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(4) *Brain and anterior of spinal cord*.—Open cranium in saline solution and tease tissue apart under dissection microscope.

(5) *Eyes*.—Examine in saline solution under the microscope and tease apart.

Artificial digest is a useful method of separation when metacercariae are not numerous or are very small, particularly when the parasite is present in muscle. It is also useful for obtaining large numbers of some metacercariae for life history and physiology studies; a few species are killed, but may be recovered intact if not left in the digesting solution too long. Usually 0.5 percent pepsin, 0.5 percent hydrochloric acid in 0.65 percent saline solution is used; the amount of acid may be varied, but more than 0.25 percent kills some metacercariae. Usually 1 percent HCl is used for mammalian tissue, but fish flesh digests more readily; the fish may be ground or cut in small pieces and placed in jars with the solution at the rate of approximately 1 gram of tissue to 20 milliliters of solution. The author uses a water shaker (Hoffman, 1955a). Nearly complete digestion of the tissue can be obtained in an hour or two by this method, but cysts in the viscera are liberated in 10 to 15 minutes. The cysts settle in 5 to 15 minutes after digestion and the supernatant fluid is then decanted; usually two rinses in the saline solution facilitates examination.

Preserved material is usually unsatisfactory because the metacercariae are contracted too much for study; intact metacercariae cannot be digested from preserved material.

Some metacercariae are freed from their cysts during the pepsin digest, and some are not; at least one species, the tetracotyle of *Apatemon pellucidus*, can be freed by following the pepsin digest with a 10-minute trypsin digest (Hoffman, 1959). The trypsin solution consists of 0.1 percent trypsin in 1 percent sodium bicarbonate.

For microscopic examination in most instances the metacercariae can best be studied alive. Anesthetics are useful, such as nicotine sulfate: 1 drop of Black Leaf 40 to 400 ml. of 0.85 percent saline solution. Menthol-tween: 0.25 percent menthol in 5 percent Tween 80, one percent chlorobutanol or 0.4 percent chloretone. Cover glass pressure is probably the best method for flattening live worms to study the excretory system. Hypertonic saline solutions are sometimes useful in studying the ex-

cretory system (L. D. Nolf, personal communication). Fixed, stained mounts are necessary for some organs. The author believes that it is best to sketch the metacercaria in its characteristic live position and fill in the details later in composite fashion from stained and mounted slides. The use of hot (nearly boiling) Bouin's solution has produced the most uniform, most nearly natural shape of the metacercariae. Hot water (65° C.), followed by formalin as used for cestode larvae by M. C. Meyer (personal communication), sometimes works equally well for metacercariae. No one method has been found to work equally well on all metacercariae. The use of PVA-AFA (polyvinyl alcohol: alcohol, formalin, and acetic acid) fixative adhesive is sometimes helpful in handling small forms (Hoffman, 1954a).

It is probable that the metacercariae of strigeoid trematodes which develop in fish-eating birds and mammals are more frequently seen, and are easier to obtain than the adult worms; it would be advantageous if they could be identified easily.

There are no comprehensive publications on the freshwater fish parasites of North America. The publications of Van Cleave and Mueller (1932, 1934) and Mueller and Van Cleave (1932) are most complete, and the fish-parasite survey publications of Bangham et al. (1933-54) and Fischthal (1947-50) are also helpful. Some excellent foreign treatises on the subject, which are helpful in studying certain groups of fish parasites, are those of Dawes (1947), Plehn (1924), Yamaguti (1933), Schäperclaus (1954), Sproston (1946), Travassos, Artigas, and Pereira (1928), and the monographs of Dubois (1938, 1953) on strigeoids.

Only key references, or those not given in Dubois (1938), are given in the following synopsis, which is arranged according to the four larval strigeoid groups found in fish. Where the adult is known the parasite is placed in the proper family, and all known stages of the parasite are discussed. If the adult is unknown, the larval species is placed in alphabetical order following the known species. In the synoptic descriptions the reserve excretory system has been slighted, not because of lack of importance, but because of lack of study. LaRue (1957) has pointed out the importance of the excretory system in the classification of trematodes, and the author suggests that further study might help in the identification and

classification of the strigeoids, particularly *Diplostomulum* and *Neascus* species.

Although the synopsis is compiled from world literature, the three keys to metacercariae from fishes are restricted to North America. The keys are entirely artificial and include location in the host, as well as morphological characteristics as aids to the identification of the strigeoids. The locations in the host were found to be consistent for the larvae studied, but some may not be specific as to location. Unless stated otherwise all measurements are in microns and were made from living material. In the following synopsis the strigeoid metacercariae are placed in four larval groups (Tetracotyle, Diplostomulum, Neascus, and Prohemistomulum), which are usually treated as

genera; that is, if the adult is not known, a strigeoid metacercaria may be placed in one of the four larval groups. If the adult is known, the metacercaria may be given the same name as the adult, or it may be given the larval group name. I prefer to use the two names in combination to avoid confusion.

I wish to thank Dr. G. R. LaRue, Animal Disease Parasite Research Branch, United States Agricultural Research Service, Beltsville, Md., for a critical review and for many helpful suggestions in the preparation of this paper, also, Dr. L. O. Nolf, University of Iowa, Dr. S. F. Snieszko and Dr. Ken Wolf, Eastern Fish Disease Laboratory, Leetown (P.O. Kearneysville, W. Va.), for reviewing the manuscript.

EXPLANATION OF FIGURES

- ACT—accessory collecting tubule.
 ALEV—anterior lateral excretory vessel.
 AN—anterior nerve.
 APCT—anterior primary collecting tubule.
 ATCV—anterior transverse commissural vessel.
 AVL—anterior of ventral lip of "cup".
 BC—bursa copulatrix.
 C—constriction between forebody and hindbody.
 CC—calcareous corpuscles.
 CCP—common collecting trunk of primary excretory system.
 CH—cavity of holdfast organ.
 CLS—cavity of lateral pseudosucker.
 CP—cirrus pouch.
 DEV—dorsolateral excretory vessel of hindbody.
 E—esophagus.
 EB—excretory bladder.
 EC—excretory canal.
 ED—excretory duct.
 EG—gelatinous globule of excretory fluid.
 ELN—network of extralateral excretory vessels.
 EMH—external meatus of holdfast.
 EO—embryonic ovary.
 EP—excretory pore.
 ET—embryonic testes.
 FB—forebody.
 GC—unicellular gland cells.
 GP—genital pore.
 GPr—genital primordium.
 H—holdfast organ.
 HB—hindbody.
 HG—holdfast gland.
 HV—holdfast vessel.
 IC—intestinal caecum.
 IL—inner lip of holdfast.
 ILEV—intralateral excretory vessel.
 J—apparent point of union of primary excretory apparatus with reserve bladder.
 LCV—lateral collecting vessel.
 LPS—lateral pseudosucker.
 M—mouth.
 MA—median anastomosis.
 MDEV—median dorsal excretory vessel.
 MEV—marginal excretory vessel.
 MLS—external meatus of lateral sucker.
 MVEV—median ventral excretory vessel.
 O—ovary.
 OI—outer lip of holdfast.
 OS—oral sucker.
 Ph—pharynx.
 PLEV—primary lateral excretory vessel.
 PLF—posterior lip of forebody.
 PN—posterior nerve.
 PPh—prepharynx.
 PPCT—posterior primary collecting tubule.
 PT—posterior tubule.
 PTCV—posterior transverse commissural excretory vessel.
 RE—reserve excretory system.
 SCV—semicircular commissural vessels.
 SPNC—suprapharyngeal nerve commissure.
 T—testes.
 TB—tubular portion of excretory bladder.
 TCV—transverse commissural vessel.
 TP EA—tubules of primary excretory apparatus.
 VEV—ventrolateral excretory vessels of hindbody.
 VS—ventral sucker.

I. TETRACOTYLE

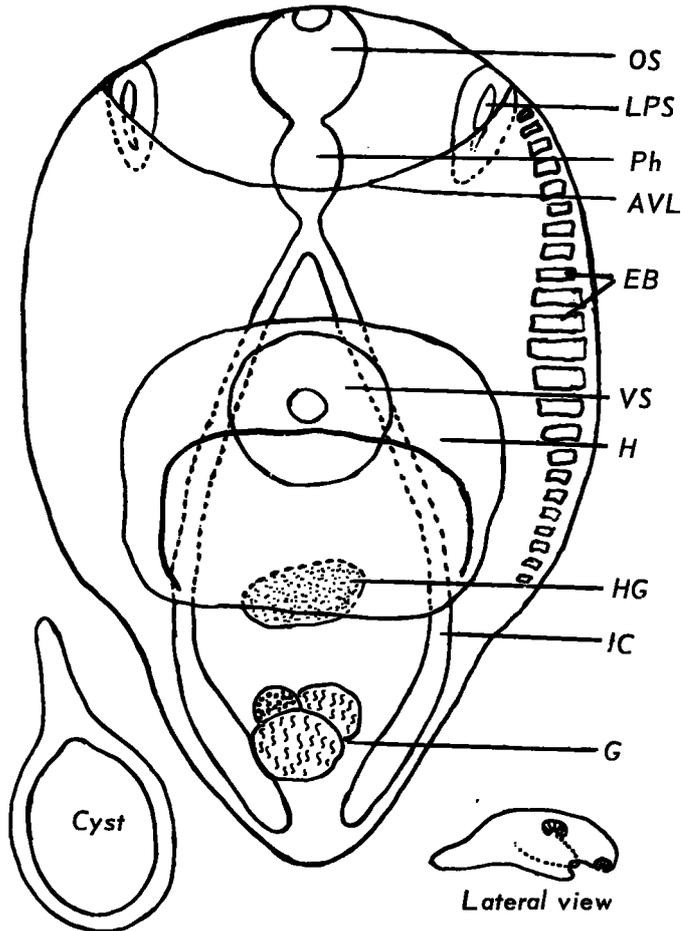


FIGURE 1.—Tetracotyle of *Apatemon gracilis pellucidus* (composite drawing from Hoffman, 1959).

This larval group has been described by Faust (1918) and Hughes (1928a, 1928d); it possesses these characteristics: (1) forebody oval or ovate-oblong in contour and relatively thick, concave ventrally or cup-shaped; (2) hindbody present as a short rounded prominence at the posterior end of the forebody, sometimes inconspicuous; (3) reserve bladder consists of a large continuous space occupying the dorsal and lateral regions of the forebody, with a sheetlike extension into the ventral lip of the anterior suctorial pocket, with small spherical calcareous concretions in the reserve excretory vessels and mostly in the anterior part of the worm; (4) a pair of lateral pseudosuckers (cotylae) on the anterolateral edges beside the oral sucker; and (5) a true cyst of parasite origin.

The last synopsis of the Tetracotyle group was by Hughes (1928d).

A. Family STRIGEIDAE Railliet.

1. *Apatemon fuligulae* Yamaguti, 1933.

Snail host and cercaria unknown.

Fish hosts: Siluridae—*Parasilurus* and *Pseudobargus*. Encysted in the skin and flesh, *Tetracotyle fuligulae* Yamaguti, 1933.

Cyst: Elongate, oval, 385 by 200 μ ; larvae easily liberated.

Metacercaria (fig. 2): Tetracotyliform; forebody long, flat, 540 by 380 μ (Yamaguti, 1933, omitted the anterior limit of the ventral surface of the forebody); hindbody stumpy, 250 by 160 μ ; oral sucker 50 μ ; lateral pseudosuckers shallow; prepharynx short; pharynx elongated, 20 μ wide; ventral sucker pre-equatorial, 60 μ long; holdfast with anterior lip which extends over ventral sucker, 160 by 240 μ ; holdfast gland

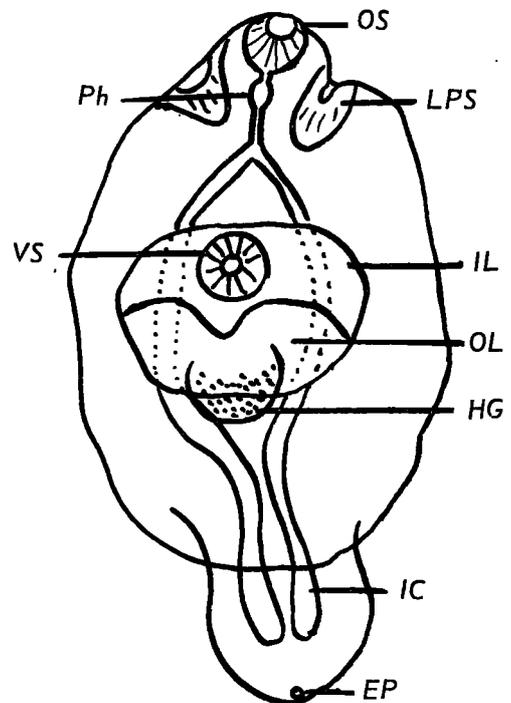


FIGURE 2.—Tetracotyle of *Apatemon fuligulae* (from Yamaguti, 1933).

prominent; genital primordia present (Yamaguti, 1933).

Final host: Anatidae—domestic duckling (experimental; Yamaguti, 1933); *Melanitta fusca stejnegeri*; *Nyroca fuligula*. Japan; Europe.

2. *Apatemon pellucidus* Yamaguti, 1933.
Snail host and cercaria unknown.

Fish host: Eleotridae—*Mogurnda obscura*. Encysted in body cavity. *Tetracotyle pelucida* Yamaguti.

Cyst: Oval, 650–700 by 500–600 μ ; host cyst fibrous, 50–80 μ thick and one end generally produced into a blunt point; difficult to liberate larva.

Metacercaria (fig. 3): Tetracotyliform; 480–750 μ long and divided into two distinct regions; forebody cup-shaped, 370–620 by 330–440 μ ; hindbody short-cylindrical, 130–200 by 150–210 μ ; esophagus short; lateral pseudosuckers deep and anterior wall

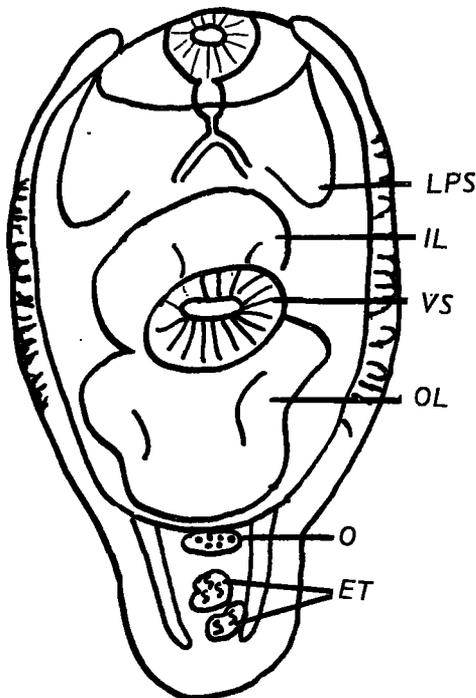


FIGURE 3.—*Tetracotyle* of *Apatemon pellucidus* (from Yamaguti, 1933).

sometimes extending forward tonguelike; ventral sucker slightly post equatorial, 80–130 by 90–140 μ ; holdfast divided into ventral and dorsal lobes; holdfast gland 30–40 by 50–60 μ ; three genital primordium bodies in hindbody; excretory system highly developed.

Final host: domestic duck (experimental). Japan.

3. *Apatemon gracilis pellucidus* (Yamaguti, 1933) Dubois, 1953.

(This may be the same species as the preceding.)

Snail host and cercaria unknown.

Fish host: Gasterosteidae—*Eucalia inconstans*. Encysted in muscle (*Tetracotyle* species, fig. 1) described in Hoffman, 1959.

Final host: Unfed chicks; (experimental). North Dakota.

4. *Cotylurus communis* (Hughes, 1928; LaRue, 1932).

Snail host unknown, cf. Olivier and Cort (1942).

Fish host: Catostomidae—*Catostomus commersonii*. Percidae—*Stizostedion canadense griseum*, *S. vitreum*. Percopsidae—*Percopsis omiscomaycus*. Encysted in pericardial cavity, *Tetracotyle communis* Hughes.

Cyst: Nearly spherical, 980–1330 μ in diameter; usually easy to free larva.

Metacercaria (fig. 4): Tetracotyliform; 570–950 by 570–900 μ ; body thick and slightly concave ventrally; hindbody very small; oral sucker 120–150 μ ; pharynx inconspicuous; esophagus short and narrow; lateral pseudosuckers smaller than oral sucker and not forming “ears” or “tongues” (i.e., not protrusible); ventral sucker 140–200 by 180–222 μ ; holdfast simple, 140–200 by 260–360 μ ; one genital primordium in hindbody.

Final host: Laridae (gulls)—*Larus argentatus*. Michigan.

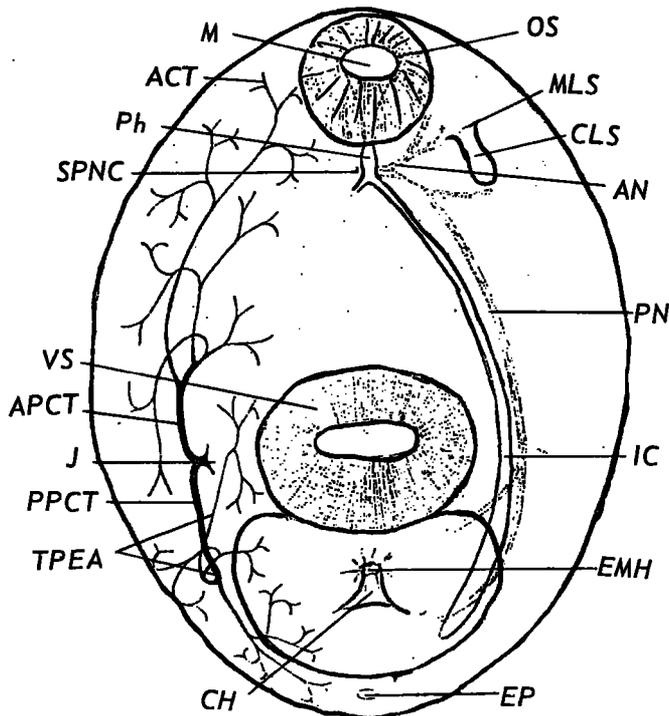


FIGURE 4.—Tetracotyle of *Cotylurus communis* showing primary excretory system (from Hughes, 1928d).

5. *Cotylurus pileatus* (Rudolphi, 1802) Dubois, 1937.

Snail host and cercaria unknown.

Fish hosts: Cyprinidae—*Abramis* species, *Alburnus alburnus*, *Phoxinus* species, *Blicca bjoerkna*. Esocidae—*Esox lucius*. Percidae—*Acerina cernua*, *Perca fluviatilis*. Encysted in the pericardial cavity, peritoneum, and eye muscles (*Tetracotyle pileata* (Rudolphi), *T. ovata*) Linst 1877, *T. variegata* (Creplin) Hughes, 1928, cf. Vickers (1951).

Cyst: Nearly spherical, ca. 1 mm. in diameter.

Metacercaria: Tetracotyliform; 840 by 570 μ ; oral sucker 98–130 μ ; ventral sucker 160–210 μ .

Final host: Alcidae—*Alca torda* (auk), *Uria aalge* = *U. troille* (murre). Laridae (gulls and terns)—*Chlidonias nigra*, *Larus* species, *L. ridibundus* (experimental), *Sterna hirundo*, *S. paradisaea*, *Thalasseus sandvicensis* = *Sterna cantiaica*. Europe, Asia.

B. Family undetermined, probably STRIGEIDAE.

6. *Tetracotyle biwaensis* Goto and Ozaki, 1930.
Fish host: Encysted in the body cavity of *Pseudogobio*. Japan (Yamaguti, 1942).

Cyst: Original description not available to author.

Metacercaria (fig. 5): Body oval, 850–950 by 550–700 μ ; oral sucker 114–130 by 120–150 μ ; pharynx 38–40 by 22–30 μ ; esophagus short; lateral pseudosuckers posterolateral to oral sucker; ventral sucker postequatatorial, 150–162 by 160–170 μ ; holdfast organ 120–180 by 200–250 μ ; genital primordium present in hindbody.

7. *Tetracotyle diminuta* Hughes, 1928.

Encysted in the pericardial cavity and adipose tissue behind eyes of *Perca flavescens* and *percopsis omiscomaycus*. Michigan.

Cyst: Ovate, 330–450 by 280–420 μ . Difficult to free larva.

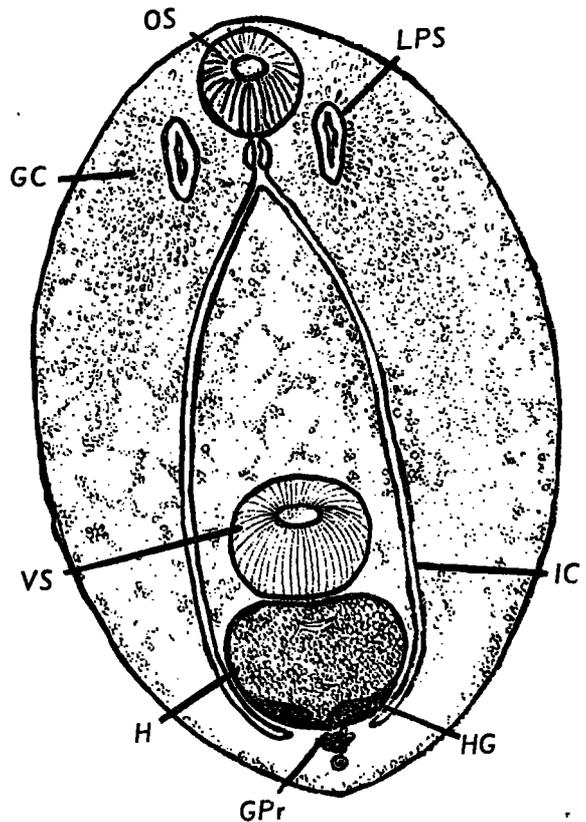


FIGURE 5.—*Tetracotyle biwaensis* (from Yamaguti, 1942).

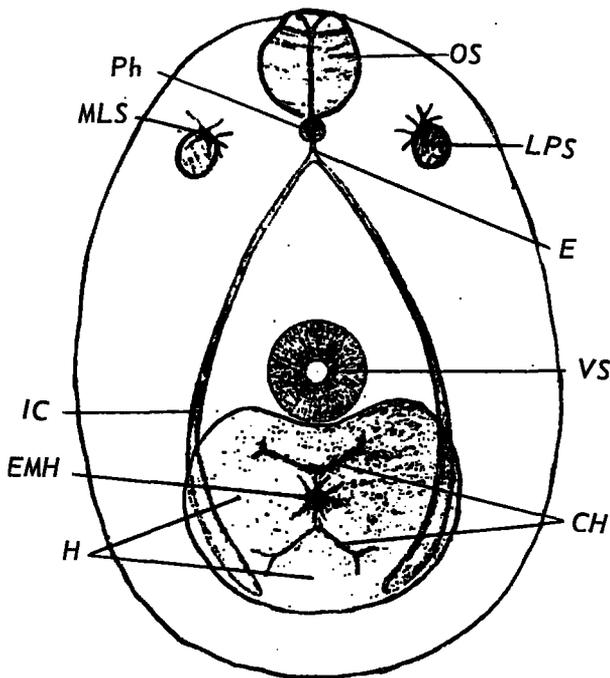


FIGURE 6.—*Tetracotyle diminuta* (from Hughes, 1928d).

Metacercaria (fig. 6): Body much like *Tetracotyle communis*. Surface appearing spinous because of mucus extrusions. 286–429 by 204–334 μ ; oral sucker 51–63 μ ; pharynx 20–23 by 15–20 μ ; esophagus short; lateral suckers deep and may be everted; ventral sucker 51–63 μ ; holdfast 78–150 by 90–180 μ ; reproductive and excretory systems similar to *Tetracotyle communis*.

8. *Tetracotyle echinata* Diesing, 1858.
Encysted in peritoneum of *Leuciscus* and *Acerina*. Europe.

Cyst: Oval 500–600 μ in diameter.

Metacercaria: Oval, 620 μ long; spines sparse, 3–4 μ long. May be mucous extrusions similar to those of *T. diminuta*. This species is characterized by the large size of the hindbody.

9. *Tetracotyle indicus* Singh, 1956.
In freshwater fish. India.

10. *Tetracotyle intermedia* Hughes, 1928.
Encysted in the pericardium of *Prosopium quadrilaterale* and *Leucichthys artedi*. Michigan.

Cyst: Ovate, 550–750 by 400–560 μ .

Metacercaria: Similar to *T. diminuta*; body 370–590 by 300–600 μ ; oral sucker 60–75 by 54–60 μ ; pharynx 24–30 by 15–18 μ ; lateral pseudosuckers similar to *T. diminuta*; ventral sucker 45–62 by 60–81 μ ; holdfast 110–116 by 150–200 μ .

11. *Tetracotyle parvulum* (*Diplostomum parvulum*) (Stafford, 1904).
May be *Cotylurus communis*; cf. Hughes (1929a).

12. *Tetracotyle percae-fluviatilis* (Moulinié) von Linstow, 1877.
Encysted in the heart region of *Percia*; Europe. Carp; Russia (Astakhova, 1953).

Metacercaria: 380–880 by 300–500 μ ; oral sucker 60 μ ; lateral suckers 66 by 133 μ ; ventral sucker inconspicuous; holdfast 80–100 μ .

13. *Tetracotyle sogdiana* Pavlovsky and Anitchkov, 1922.
Encysted in pancreas of *Schizothorax*. Turkestan.

Metacercaria: Ventral sucker anterior to the middle of the body; longitudinal invaginations in dorsal body wall.

14. *Tetracotyle sophoriensis* Singh, 1956.
In fresh water fish; India.

15. *Tetracotyle tahoensis* Haderlie, 1953.
Encysted in the pericardium of *Catostomus tahoensis*. California.

Cyst: Spherical, yellow or straw colored; ca. 630 μ in diameter (fixed specimen) worms easily freed.

Metacercaria (fig. 7): 520–740 by 350–490 μ ; oral sucker 100–120 μ ; pharynx indistinct; lateral suckers ventrally located, ca. 110 μ in diameter; ventral sucker 80–110 by 130–150 μ ; holdfast 120–140 by 160–170 μ ; genital primordium a small, single mass (fixed specimens).

16. *Tetracotyle* species.

Reported from many fishes by Bangham (1944), Wisconsin (1951), Wyoming (1955), Lake Huron; Bangham and Adams (1954), British Columbia; Bangham and Venard (1942), Tennessee; Fischthal (1947a, 1947b, 1950), Wisconsin; Hunter (1942), Connecticut; Sinderman (1953), Massachusetts; Van Cleave and Mueller (1934), New York; Yamaguti (1942), Japan.

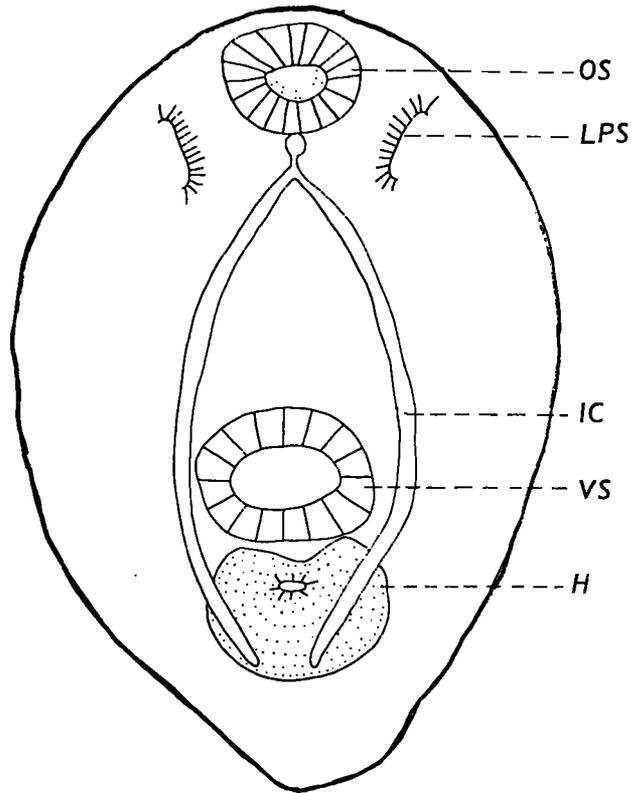


FIGURE 7.—*Tetracotyle tahoensis* (from Haderlie, 1953).

KEY TO THE KNOWN SPECIES OF TETRACOTYLE OF NORTH AMERICAN FISH

Undoubtedly there are many undescribed species of *Tetracotyle*.

1. Cyst with a prominent tail-like projection; found in musculature of *Eucalia inconstans*.....*Apatemon pellucidus*
1. Cyst without a prominent tail-like projection; not found in musculature but found in viscera, particularly pericardium
2. Lateral cotylae as large as oral sucker.....*T. tahoensis*
2. Lateral cotylae decidedly smaller than oral sucker..... 3
3. Diameter of holdfast organ about one-half to one-third the total length of the parasite; difficult to remove parasite from its cyst.....*T. dimjvuta*
3. Diameter of holdfast organ less than one-third the total length of the parasite..... 4
4. Intact cyst about 1000 μ in diameter; parasite about 700 μ long; pharynx observed with difficulty; parasite easily freed from cyst.....*Cotylurus communis*
4. Intact cyst about 600 μ in diameter; parasite about 450 μ long; pharynx easily seen.....*T. intermedia*

II. DIPLOSTOMULUM

This larval group has been described by Hughes (1929a) and possesses these characteristics: (1) forebody foliaceous, concave ventrally; (2) hindbody present as a small conical prominence on the posterodorsal part of the forebody; (3) reserve system (bladder) consists of a system of more or

less definitely arranged tubules with calcareous corpuscles, round or ellipsoidal, disposed in vesicles at the termini of small branches; (4) usually a pair of lateral organs (the so-called lateral suckers) on the anterolateral edges beside the oral sucker; and (5) no true cyst of parasite origin.

The last synopsis was that of Hughes (1929a).

Final host: Wild mallard duck; experimental in unfed chick (Hoffman, 1955b; Hoffman and Hundley, 1957), North Dakota.

3. *Diplostomum flexicaudum* (Cort and Brooks, 1928) Van Haitma, 1931.

Snail hosts: *Stagnicola* species; (*Cercaria emarginata* Cort), *Fossaria*, *Stagnicola*, *Lymnaea* (Cort, Hussey, and Ameel, 1957). Precocious metacercaria in snail (Olivier, 1940).

Fish hosts: Catostomidae—*Catostomus* species. Centrarchidae—*Lepomis macrochirus* (experimental; Ferguson, 1943b). Cyprinidae—*Pimephales promelas* (experimental; Ferguson, 1943b). Salmonidae—*Salmo irideus* (experimental; Ferguson, 1943b); experimental in tadpoles, frogs, turtles, chicks, ducklings, mice, rats, guinea pigs, and rabbits, (Olivier, 1940; Ferguson, 1943b). Lens of the eye [*Diplostomulum flexi-*

caudum (Cort and Brooks), (*D. gigas* Hughes and Berkhout, 1929)].

Metacercaria (fig. 10): 500–900 by 400–450 μ ; hindbody ca. 100 μ long; oral sucker 80–90 μ ; pharynx 60 by 23 μ ; ventral sucker 90 μ .

Final host: Laridae (gulls)—*Larus argentatus*. Michigan; Minnesota.

4. *Diplostomum huronense* (LaRue, 1927) Hughes and Hall, 1929.

Snail host and cercaria unknown.

Fish hosts: Percidae—*Perca flavescens*. Percopsidae—*Percopsis omiscomaycus*. Eyes [*Diplostomulum huronense* (LaRue) Hughes and Hall].

Metacercaria (fig. 11): 280–600 by 100–150 μ ; hindbody ca. 90 μ long; oral sucker 40–50 by 28–40 μ ; pharynx 35–40 by 26–28 μ ; ventral sucker 35–40 μ ; holdfast 50–80 by 70–80 μ .

Final host: Laridae (gulls)—*Larus argentatus*. Michigan.

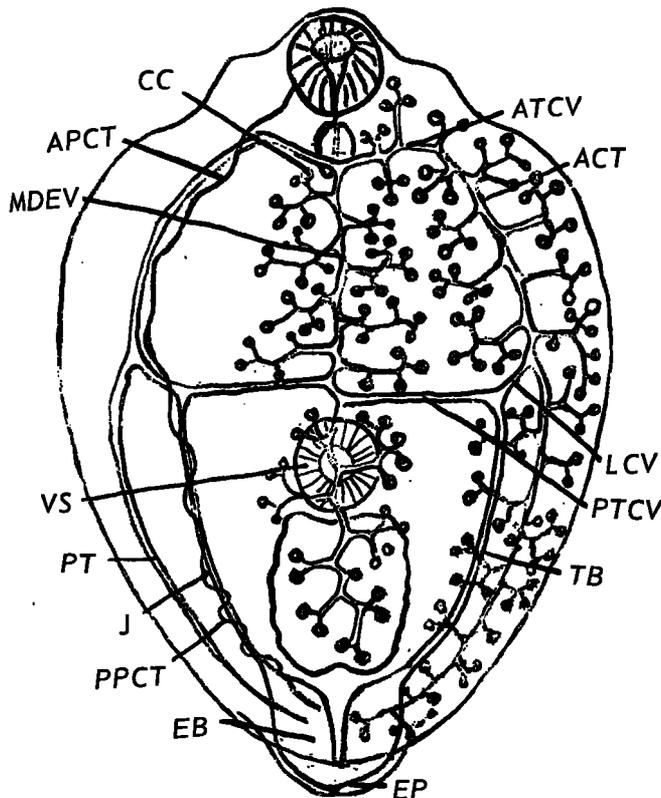


FIGURE 10.—Diplostomulum of *Diplostomum flexicaudum* showing reserve excretory system and associated calcareous corpuscles (from Hughes and Berkout, 1929).

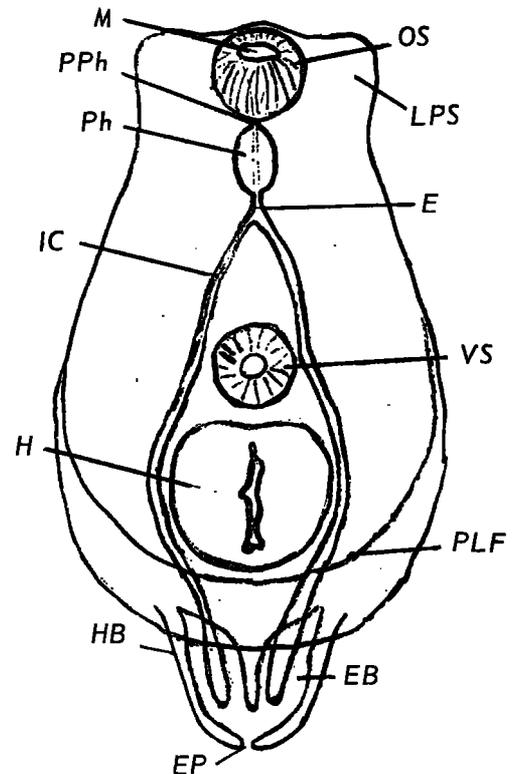


FIGURE 11.—Diplostomulum of *Diplostomum huronense* (from Hughes and Hall, 1929).

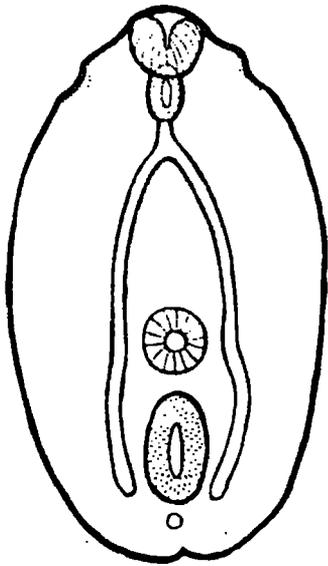


FIGURE 12.—Diplostomulum of *Diplostomum murrayense* (from Johnston and Angel, 1941).

5. *Diplostomum murrayense* Johnston and Angel, 1941.

Snail host: *Limnea lissoni*.

Fish hosts: Many species; in eyes.

Metacercaria (fig. 12): Original description (Johnston and Simpson, 1939) not seen by author.

Final host: Laridae—*Chlidonias leucopareia* (tern). Australia. (Johnston and Angel, 1941).

6. *Diplostomum palmatoides* Dubois, 1932.

Erroneously reported as the adult of *Diplostomulum phoxini* by Rees (1955). See *Diplostomum phoxini*.

7. *Diplostomum phoxini* (Faust, 1918) Arvy and Buttner, 1954.

Snail host: *Lymnaea* species (Arvy and Buttner, 1954; Rees, 1957).

Fish host: Cyprinidae—*Phoxinus* species. Unencysted in brain, [*Diplostomulum phoxini* (Faust) Ashworth and Bannerman, 1927].

Metacercaria (figs. 13, 14): Body with two distinct regions, 247–344 by 130–215 μ ; spine-like striations in cuticle; oral sucker

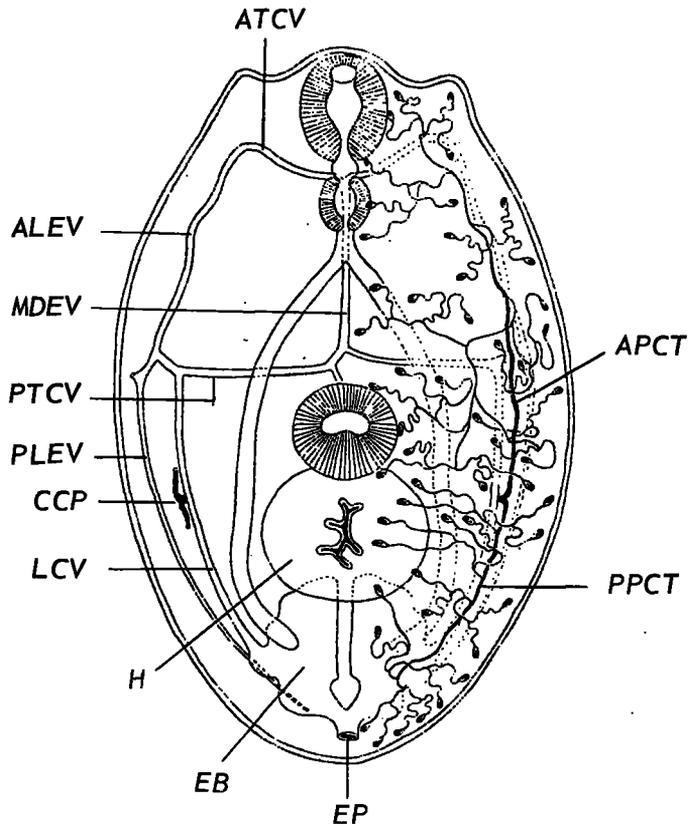


FIGURE 13.—Diplostomulum of *Diplostomum phoxini* showing primary excretory system (black) and reserve excretory system (from Rees, 1955). Note: normal shape probably similar to that of *D. baeri eucaliae* (fig. 9).

46 by 41 μ ; prepharynx small; esophagus short; lateral pseudosuckers prominent; ventral sucker 43 by 50 μ ; holdfast 66 by 83 μ ; calcareous corpuscles spherical or ovoid, 6–12 μ in greatest diameter (Rees 1955); experimental in domestic duck. Arvy and Buttner, 1954. France. Bell and Hopkins, 1956; Rees 1955. England.

8. *Diplostomum spathaceum* (Rudolphi, 1819) Braun, 1893.

Snail host: *Lymnaea* species (*Cercaria C.* of Szidat) (Dawes, 1952).

Fish hosts: Acipenseridae—*Acipenser nudiiventris*. Anguillidae—*Anguilla anguilla*. Centrarchidae—*Micropterus dolomieu*. Cichlidae—*Cichlasoma aureum* (Mexico—Caballero and Winter, 1954). Cobitidae—*Cobitis* species. Cyprinidae—*Abramis* species.

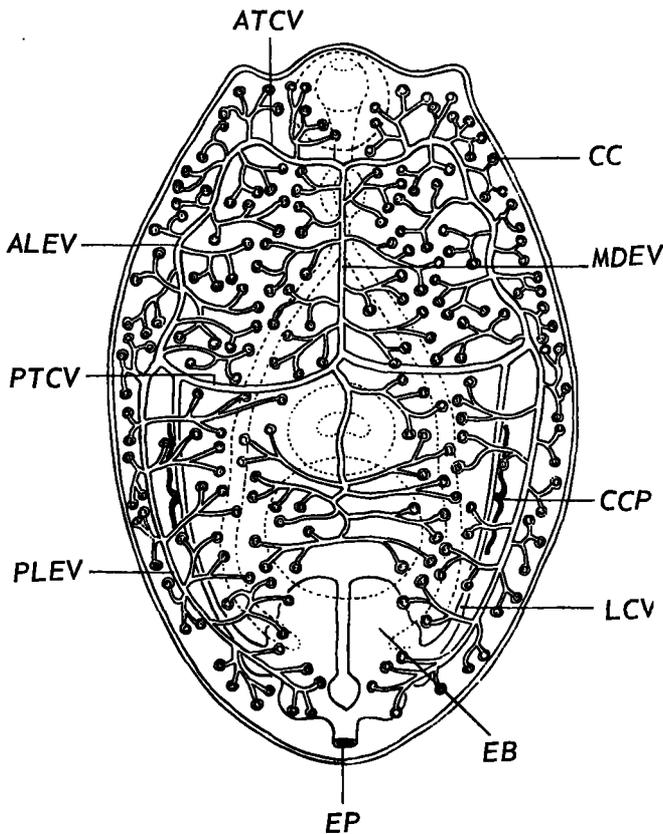


FIGURE 14.—Diplostomulum of *Diplostomum phoxini* showing reserve excretory system and associated calcareous corpuscles (from Rees, 1955).

Aspius a. erythrostomus, *Barbus* species, *Capoetobrama juschakewitschi*, *Carassius auratus gibelio*, *Chalcalburnus chalcoides*, *Chondrostoma nasus*, *Cyprinus carpio*, *Gobio fluviatilis*, *Leuciscus* species, *Pelecus cultratus*, *Phoxinus phoxinus*, *Scardinius erythrophthalmus*, *Squalius* species. Cottidae—*Cottus gobio*. Esocidae—*Esox lucius*. Gadidae—*Lota lota*. Gasterosteidae—*Gasterosteus aculeatus*, *G. pungitius*, *Pyrosteus platygaster*. Salmonidae—*Coregonus* species, *Salmo* species, *Thymallus thymallus*. Siluridae—*Silurus glanis*. Eyes (lens and vitreous humor) [*Diplostomulum spathaceum* (Rudolphi), Hughes 1929].

Metacercaria: Original descriptions not studied.

Final hosts: Alcidae—*Alca torda* (auk). Laridae (gulls and terns)—*Larus* species, *Rissa*

tridactyla, *Stercorarius parasiticus*. Pelecanidae—*Morus bassanus*. Europe.

9. *Hysteromorpha triloba* (Rudolphi, 1819) Lutz, 1931.

Snail host: *Gyraulus hirsutus*, *Cercaria Hysteromorpha trilobae* Huggins, 1954.

Fish hosts: Cyprinidae—*Abramis* species, *Hyborhynchus notatus*, *Idus idus*, *Leuciscus* species, *Tinca tinca*. Poeciliidae—*Poecilia vivipara*. Siluridae—*Ameiurus* species. Encysted in the musculature. (*Diplostomulum corti*) and (*D. trilobum*).

Host cyst: Delicate fibrous host cyst, 990–1320 by 830–1160 μ .

Metacercaria (fig. 15): with two distinct body regions; body 1520 by 450 μ (Huggins, 1954). Body 700–880 by 400–350 μ ; oral sucker 62–72 μ ; pharynx 40–53 by 26–38 μ ; esophagus 15–21 μ ; lateral pseudosuckers deeply cupped; ventral sucker 73–86 μ , pre-equatorial; holdfast trilobate; holdfast gland well developed; genital primordia well developed [fixed specimens (Hughes, 1929a).] European measurements slightly larger; cf. Dubois (1938).

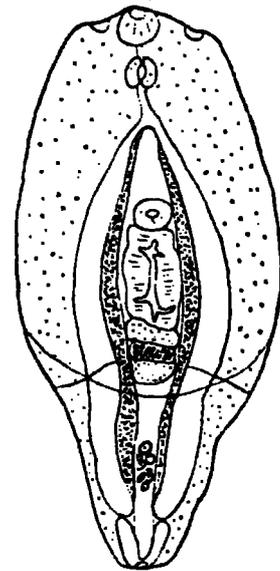


FIGURE 15.—Diplostomulum of *Hysteromorpha triloba* (from Huggins, 1954).

Final hosts: Ardeidae (herons); *Ardea* species, *Nyctinassa* species, *Egretta* species (non-ovigerous adults; experimental). Phalacrocoracidae (cormorant)—*Phalacrocorax* species; unfed chick (experimental, North Dakota, Hoffman, this paper). Australia, Austria, Brazil, Japan, Romania, Manitoba (Canada); Illinois, Michigan, Minnesota, Wisconsin (U.S.A.), cf. Huggins, 1954.

10. *Tylodelphys clavata* (von Nordmann, 1932)
Diesing, 1850.

Snail host and cercaria unknown.

Fish hosts: Cyprinidae—*Abramis* species, *Barbus branchycephalus*, *Carassius carassius*, *Leuciscus* species, *Scardinius erythrophthalmus*, *Tinca tinca*, *Aspius aspius*, *Chalcaburnus chaloides*. Esocidae—*Esox lucius*. Percidae—*Acerina cernua*, *Lucioperca volgensis*, *Perca fluviatilis*, *Sandra lucioperca*, *Aspro streber*. Salmonidae—*Coregonus* species. Vitreous humor [*Diplostomulum clavatus* (von Nordmann) Faust].

Metacercaria: Body elongate, length more than twice its width; lateral pseudosuckers sometimes "everted"; hindbody not clearly set off from forebody; body 310–520 by 100–150 μ ; oral sucker 41 by 33 μ ; prepharynx 11 μ ; pharynx 24 by 15 μ ; esophagus 33 μ ; ventral sucker 24 μ ; holdfast 59 by 37 μ ; excretory bladder Y-shaped and large [cf. Dubois (1938)].

B. Family undetermined, probably Diplostomatidae.

11. *Diplostomulum craniarium* (Diesing, 1850).
Cranial cavity of *Cobitis*. Europe. Reported only once.

12. *Diplostomulum (Tylodelphys?) destructor*
Szidat and Nani, 1951.

Snail host: *Planorbis*. Cercaria similar to *Tylodelphys excavata*.

Fish hosts: Brain of *Basilichthys* species, *Fitzroya*, and *Salmo*. Argentina.

Metacercaria (fig. 16): Body 830 by 250 μ ; oral sucker 42 μ ; pharynx 40 by 16 μ ; lateral

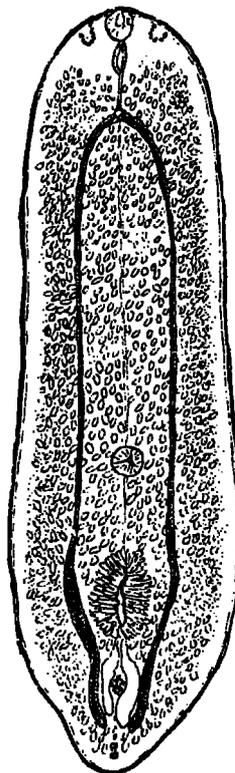


FIGURE 16.—*Diplostomulum (Tylodelphys?) destructor*
(from Szidat and Nani, 1951).

suckers not prominent; ventral sucker 42 μ ; holdfast 140 by 80 μ ; calcareous corpuscles oval [Szidat and Nani, 1951].

13. *Diplostomulum elongatus* Singh, 1957.

Fish host: Encysted on mesenteries of the Indian freshwater fish, *Trichogaster fasciatus*.

Host cyst: 1,020 by 670 μ .

Metacercaria (fig. 17): Elongate, aspinose, body division not distinct; forebody 972 by 558 μ ; hindbody 200 μ long; oral sucker 45 μ ; no prepharynx; pharynx 30 μ in diameter; esophagus short; lateral pseudosuckers not prominent, posterolateral to oral sucker; ventral sucker 70 by 40 μ ; holdfast much posterior to ventral sucker, 136 μ in diameter; holdfast gland 132 by 30 μ ; genital primordia present; no calcareous corpuscles.

14. *Diplostomulum emarginatae* Olivier, 1942.
Similar to *D. flexicaudum*.

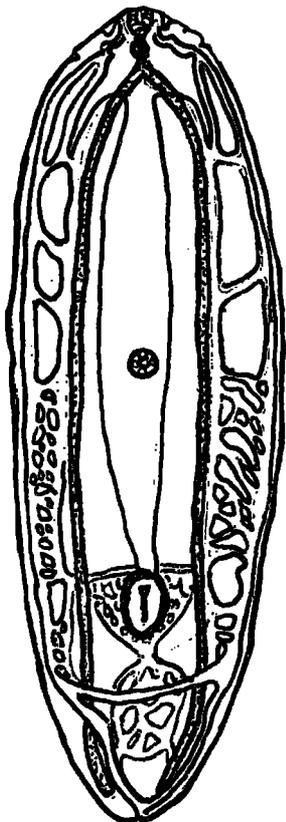


FIGURE 17.—*Diplostomulum elongatus* showing reserve excretory system (from Singh, 1957).

15. *Diplostomulum heterobranchi* (Wedl).

Fish host: In adipose tissue about brain of *Heterobranchius anguillarvis*. Egypt.

16. *Diplostomulum ictaluri* Haderlie, 1953.

Fish host: Flesh of *Ictalurus catus*. California.

Host cyst: White, fibrous, and slightly spindle-shaped, ca. 1,500 by 950 μ . Larva difficult to remove.

Metacercaria (fig. 18): Body regions indistinct; body 1,400-1,710 by 560-770 μ ; anterior end distinctly cone-shaped; oral sucker 60-90 μ ; no prepharynx; pharynx ca. 37 μ ; ventral sucker poorly defined, 40 μ in diameter; holdfast 210 by 120 μ ; calcareous corpuscles round [fixed and stained (Haderlie, 1953)].

17. *Diplostomulum lenticola* (von Linstow, 1878).

Fish host: Lens of *Abramis*. Europe.

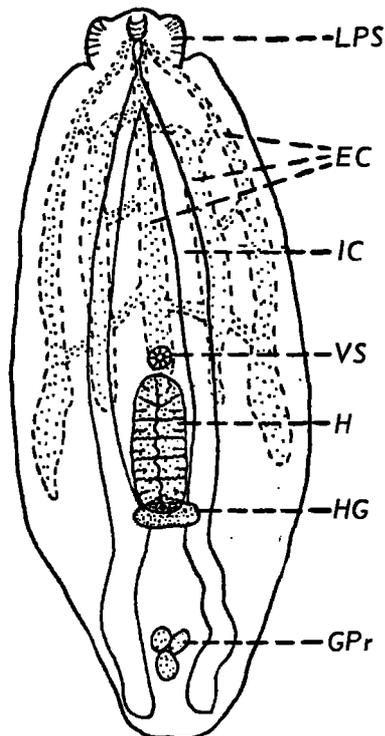


Figure 18.—*Diplostomulum ictaluri* (from Haderlie, 1953).

Metacercaria: Body outline broadly pyriform, 550 by 460 μ ; oral sucker 66 μ ; lateral pseudosuckers at extreme anterolateral reaches; ventral sucker present; holdfast 66 μ .

18. *Diplostomulum metadena* Johnston and Angel, 1942.

Snail host: *Amerianna* species (also precocious metacercaria in small snail host).

Fish hosts: Natural in subcutaneous tissue of *Craterocephalus fluviatilis* and *Mugilogobius galwayi*. Experimentally in *Gambusia affinis* and *Phalloceros caudomaculatus*. Australia.

Host cyst: Thin, ovoid, 1,000-1,200 by 520-580 μ . Larva easily freed.

Metacercaria (fig. 19): Body 880 by 300 μ average; oral sucker 36 μ ; pharynx smaller than oral sucker; lateral pseudosuckers shallow but protrusible; ventral sucker ca. 25 by 20 μ ; holdfast ca. 120 by 80 μ ; genital

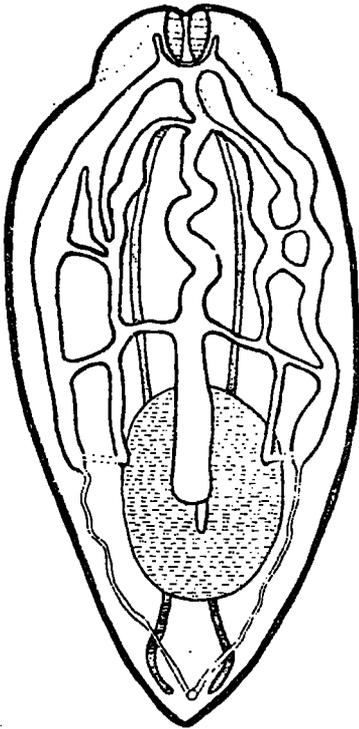


Figure 19.—*Diplostomulum metaena* showing reserve excretory system (from Johnston and Angel, 1942) [This specimen is flattened slightly.]

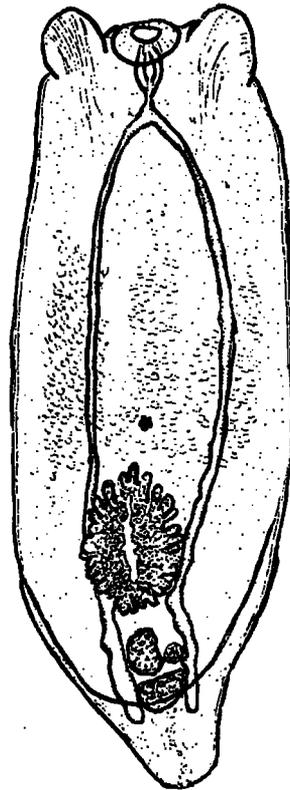


FIGURE 20.—*Diplostomulum mordax* (from Szidat and Nani, 1951).

primordia not well developed; calcareous corpuscles wanting (fixed and stained).

Final host: Adult (possibly is *Bolbophorus* of pelican).

19. *Diplostomulum mordax* Szidat and Nani, 1951.

Fish host: Brain of *Basilichthys* species.

Metacercaria (fig. 20): Body 680–880 by 330 μ ; oral sucker 50–80 μ ; pharynx 30 by 50 μ ; ventral sucker indistinct; genital primordia well formed (Szidat and Nani, 1951).

Final host: Szidat and Nani suggest that the adult is *Austrodiplostomum mordax* from *Phalacrocorax*. Argentina.

20. *Diplostomulum petromyzi-fluviatilis* (Diesing, 1850).

Cyclostome host: Cranial cavity of *Petromyzon* species. Europe.

Metacercaria: Body 225–289 by 211–261 μ ; oral sucker 42–53 μ ; pharynx 31–49 by 17–25 μ ; cavity of lateral pseudosuckers 24–35 μ deep, often spectacularly everted anteriorly; holdfast 63–109 by 105–112 μ [fixed and stained (Hughes, 1929a)].

21. *Diplostomulum scheuringi* Hughes, 1929.

Has been recorded from the vitreous humor of eyes of fishes of the families Centrarchidae, Cyprinidae, Esocidae, Etheostomidae, Gadidae, Percidae, Percopsidae, Salmonidae and Siluridae by Bangham (1944), Wisconsin. Chandler (1951), Minnesota. Fischthal (1947b, 1950), Wisconsin. Haderlie (1953). Free in the coelom. California. Hughes (1929b), Michigan. Hunter (1942), Connecticut. Mueller and Van Cleave (1931), New York. Palmer (1939), Sinderman (1953), Massachusetts.

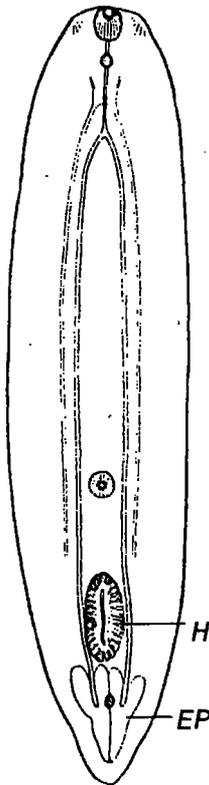


FIGURE 21.—*Diplostomulum schearingi* (from Van Cleave and Mueller, 1934).

Metacercaria (fig. 21): Closely resembles *D. clavatum*; body length more than twice the width, ventral surface only slightly concave; lateral suckers and hindbody poorly differentiated; calcareous corpuscles ellipsoidal; body 885–1,155 by 210–270 μ ; oral sucker 30–45 μ ; ventral sucker 36–45 μ ; holdfast 96–150 by 42–75 μ [fixed specimens (Hughes, 1929)].

22. *Diplostomulum truttae* Lal, 1953.

Fish host: Eyes of *Salmo trutta*. Scotland.

Metacercaria (fig. 22): Body ca. 1,000 μ long and covered with minute papillae; forebody large; oral sucker 110 μ ; prepharynx short; esophagus short; lateral pseudosuckers deeply cupped and eversible; ventral sucker 75 μ , smaller than oral sucker; holdfast well developed; calcareous corpuscles spherical.

23. *Diplostomulum* species.

Recorded from the eyes of many species of

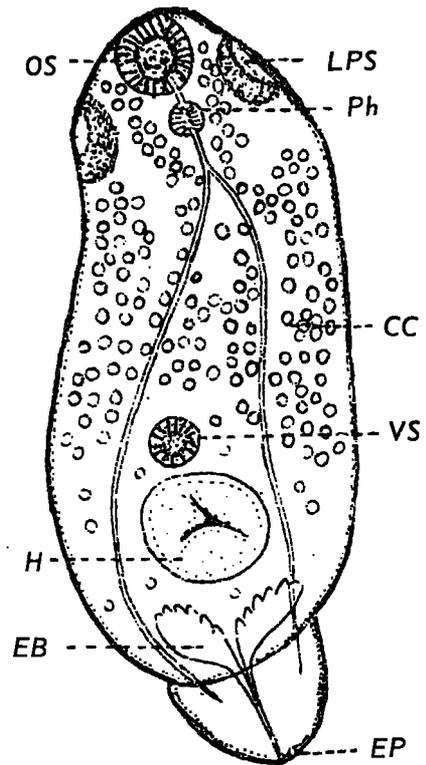


FIGURE 22.—*Diplostomulum truttae* (from Lal, 1953).

fish; it is often difficult to make a more specific identification.

KEY TO THE KNOWN *DIPLOSTOMULUM* SPECIES OF NORTH AMERICAN FRESH-WATER FISH

Undoubtedly there are many undescribed species of *Diplostomulum*.

1. Found in eyes; hindbody indistinct (except *Diplostomulum spathaceum*)----- 2
1. Found in the musculature or brain; hindbody distinct ----- 5
2. Hindbody distinct-- *Diplostomulum spathaceum*
2. Hindbody very small or not apparent----- 3
3. Found in the lens-- *Diplostomulum flexicaudum*
3. Found in the vitreous humor----- 4
4. Worm three times as long as broad.
Diplostomulum schearingi
4. Worm less than three times as long as broad ----- *Diplostomulum huronense*
5. Found in the brain of *Eucalia inconstans*-----
Diplostomulum baeri eucaliae

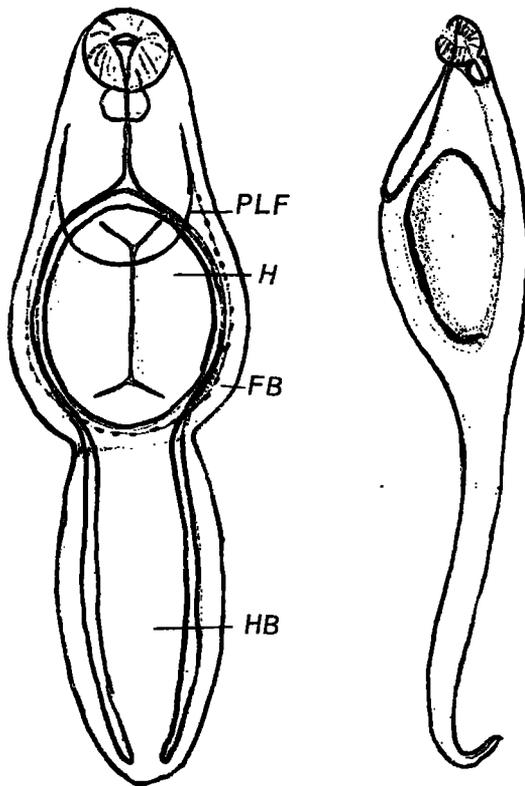


FIGURE 24.—*Neascus* of *Crassiphiala bulboglossa* (from Hughes, 1928c).

Host cyst: Pigmented, 360–680 μ .

Parasite cyst: Ovate, 180–220 by 140–180 μ ; parasite folded and filling cyst; difficult to remove parasite without using enzymes.

Metacercaria (fig. 24): Two distinct body regions; body 310–400 by 125–174 μ ; forebody deeply cupped, 167–218 μ long; hindbody conical; oral sucker 39–45 μ ; pharynx 21–24 μ ; esophagus long; ventral sucker wanting; holdfast 84–111 μ long; holdfast gland wanting; genital primordia wanting (Hughes, 1928c).

Final host: Alcedinidae (kingfishers)—*Ceryle alcyon*. North Dakota and elsewhere (cf. Hoffman, 1956).

2. *Mesophorodiplostomum pricei* (*Neodiplostomum pricei*) (Krull, 1934) Dubois, 1936.
Snail host and cercaria unknown.

Fish host: *Fundulus* spp. [*(Neascus pricei)* Krull, 1934]. No description of the metacercaria was published.

Final host: Laridae (gulls)—*Larus* species (experimental). United States.

3. *Neodiplostomum perlatum* (Ciurea, 1911), 1929.

Snail host and cercaria unknown.

Fish host: Cyprinidae—*Cyprinus carpio*. Encysted in the fins and musculature [*Neascus perlatus* Ciurea (1911) 1929].

Cyst: Spherical to slightly ellipsoidal, pearl-like, 1,820–2,300 by 1,680–1,980 μ .

Metacercaria (fig. 25): Forebody 910–940 by 540–670 μ ; hindbody 260 by 290–340 μ ; oral sucker 77–88 μ ; pharynx 59–66 by 44–55 μ ; ventral sucker 66–77 μ ; holdfast 130–180 μ .

Final hosts: Accipitridae (hawks)—*Circus aeruginosus* (experimental); *Haliaeetus albicilla*; *Falco subbuteo*; *Milvus migrans* (experimental). Romania.

4. *Ornithodiplostomum ptychocheilus* (Faust, 1917) Dubois, 1936.

Snail host: *Physa* species (Hoffman, 1958b).

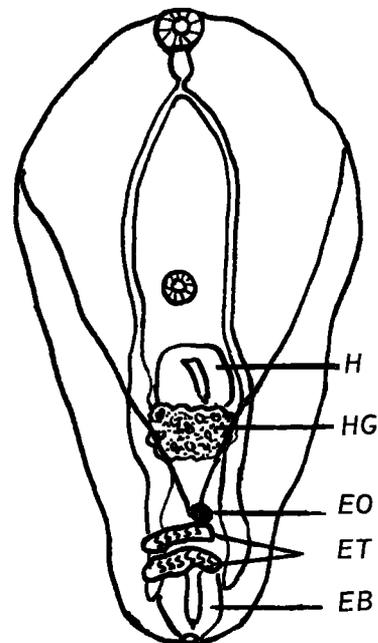


FIGURE 25.—*Neascus* of *Neodiplostomum perlatum* (from Ciurea, 1930).

Fish hosts: Cyprinidae—*Notropis* species, *Pimephales promelas*, *Ptychocheilus oregonensis*, *Semotilus a. atromaculatus*. Encysted in the peritoneum, viscera, and cysts free in the ovaries; on the brain of some species. [*Neascus ptychocheilus* (Faust) Hughes and Piszczek, 1928.]

Cyst: Often much larger than parasite, oval, 675–900 by 400–630 μ .

Metacercaria (fig. 23): Very similar to *Posthodiplostomum minimum* but smaller and strigeoid constriction very shallow; forebody lacks a distinct posteroventral lip, concavity shallow or wanting; hindbody short and broad; body 548–847 by 245–399 μ ; oral sucker 28–37 μ ; pharynx 28–40 μ ; ventral sucker 35–42 by 35–45 μ ; holdfast 76–88 by 96–106 μ .

Final hosts: Anatidae (ducks) — *Harelda hyemalis*, *Lophodytes cucullatus*, *Mergus* species; ducklings (experimental). Ardeidae—(herons) *Botaurus lentiginosus*, (Hoffman, 1956b); unfed chick (experimental) Hoffman, 1954. Illinois, Michigan, Montana, North Dakota.

5. *Posthodiplostomum cuticola* (von Nordmann, 1832) Dubois, 1936.

Snail host and cercaria unknown.

Fish hosts: Acipenseridae—*Acipenser nudi-ventris*. Cobitidae—*Cobitis taenia*. Cyprinidae—*Abramis* species, *Barbus brachycephalus*, *Capoetobrama kuschake-witschi*, *Carassius auratus gibelio*, *Chondrostoma nasus*, *Cyprinus carpio*, *Gobio gobio*, *Leuciscus* species, *Phoxinus phoxinus*, *Squalius cephalus*, *Aspius a. erythrostomus*, *Chalcalburnus chalcoides*, *Pelecus cultratus*. Percidae—*Perca fluviatilis*. Siluridae—*Silurus glanis*. Black cysts in the skin, superficial musculature, gills, mouth, fins, cornea of eye. [*Neascus cuticola* (von Nordmann) Hughes, 1927].

Cyst: Ovoid to spherical, pigmented, 690–990 μ .

Metacercaria (fig. 26): Body 730–1,980 μ ; forebody 610–820 by 390–660 μ ; hindbody

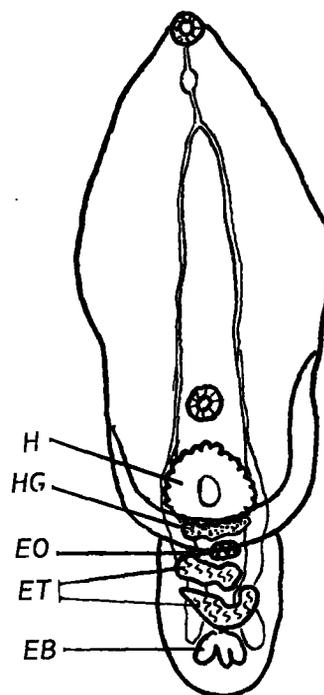


FIGURE 26.—*Neascus* of *Posthodiplostomum cuticola* (from Ciurea, 1930).

290–420 by 290–490 μ ; oral sucker 63–77 by 55–61 μ ; prepharynx 22 μ ; pharynx 55–61 by 30–37 μ ; esophagus 22–55 μ ; ventral sucker 68–77 μ ; holdfast 120–140 μ .

Final hosts: Ardeidae (herons)—*Ardea* species, *Ardeola ralloides*, *Egretta garzetta*, *Nycticorax nycticorax*. Europe.

6. *Posthodiplostomum minimum centrarchi* (MacCallum, 1921; Dubois, 1936) Hoffman, 1958.

Snail hosts: *Physa* species, Cercaria of *Posthodiplostomum minimum* Miller, 1954. (*Cercaria louisiana* Miller, 1936 = *C. multicellulata* of Ferguson, 1936; Hunter and Hunter, 1940).

Fish hosts: Centrarchidae: except *Micropterus salmoides*, perhaps others (cf. Hoffman, 1958a). Encysted in kidneys, liver, pericardium, and spleen [*Neascus vanceleavei* (Agersborg) Hughes, 1928].

Cyst: Usually longer than larva, 1,050–1,450 by 650–750 μ .

Metacercaria (figs. 27a, 27b): Two distinct body regions; body 910–2,240 μ ; forebody 520–890 by 300–420 μ ; hindbody conical to spheroidal; oral sucker 31 μ ; prepharynx short; pharynx 23 μ long; ventral sucker 46–62 μ ; holdfast 120–150 μ in diameter; genital primordium well formed (Hughes, 1928b).

Final hosts: Ardeidae (herons)—*Ardea* species, *Butorides vivescens*, *Herodias egretta*, *Nycticorax nycticorax* (experimental); Gaviidae (loons) *Gavia immer* (see Ferguson, 1937); unfed chicks, experimental (Ferguson, 1937; Hoffman, 1958a); United States, Canada, Cuba (Perez Viguera, 1944).

7. *Posthodiplostomum minimum minimum* (MacCallum, 1921; Dubois, 1936) Hoffman, 1958a.

Snail host: *Physa* species (cf. Hoffman, 1958a).

Fish host: Cyprinidae (cf. Hoffman, 1958a).

Encysted in the mesenteries [*Neascus van-cleavei* (Agersborg) Hughes, 1928]. Very similar to *P. m. centrarchi* but smaller.

Final hosts: As above (6) perhaps (records for above are for *P. minimum*); it is not known which subspecies was concerned except for *Nycticorax*, which Ferguson experimentally infected with both strains. United States.

8. *Uvulifer ambloplitis* (Hughes, 1927), Dubois, 1938.

Snail hosts: *Helisoma campanulatum*, *Helisoma trivolvis*. (*Cercaria bessiae* Cort and Brooks). Possibly *C. flexicorpa* Collins, 1935.

Fish hosts: Centrarchidae—*Ambloplites rupestris*, *Enneacanthus obesus*, *Micropterus salmoides*, *Lepomis* species, *Micropterus dolomieu*, *Pomoxis* species, *Scelerotis punctatus*.

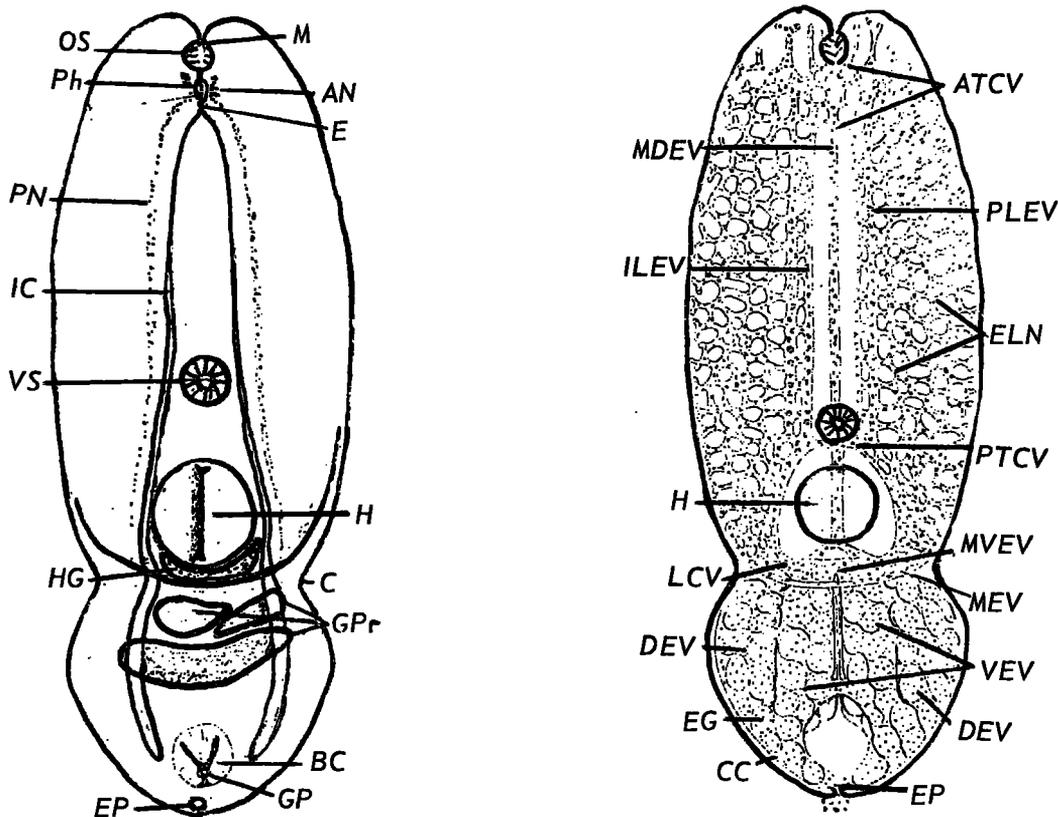


FIGURE 27.—*Neascus* of *Posthodiplostomum minimum* (from Hughes, 1928b). Normal shape is more like that in figure 24. Reserve excretory system shown on right.

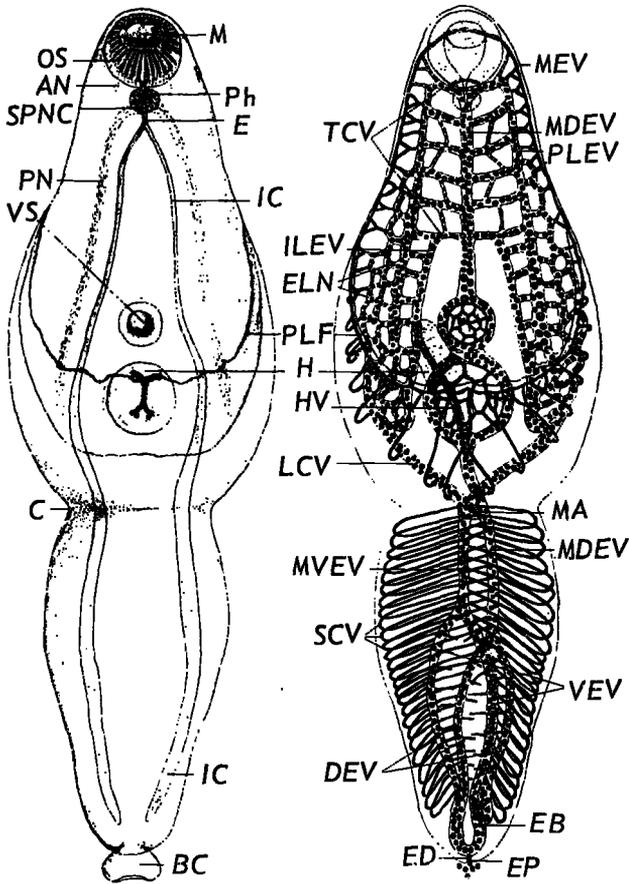


FIGURE 28.—*Neascus* of *Uvulifer ambloplitis* (from Hughes, 1927). Reserve excretory system shown on right.

tatus. Cyprinidae—*Chrosomus erythrogaster*, *Hybognathus hankinsoni*, *Hyborhynchus notatus*, *Margariscus margarita*, *Notemigonus chrysoléucas*, *Notropis* species, *Pfrille neogaea*, *Pimephales promelas*. Esocidae—*Esox* species. Black cysts in skin, myotomes, base of fins, around eyes, and in mouth (*Neascus ambloplitis* Hughes, 1927).

Host cyst: Pigmented.

Parasite cyst: Pyriform, distinctly flattened dorsoventrally, 360–390 by 172–236 μ ; difficult to free larva; parasite fills cyst.

Metacercaria (fig. 28): Two distinct body regions; forebody very thin, leaflike and deeply spoon-shaped, ventral surface spinous; 225–675 by 150–232 μ ; hindbody conical, 187–675 by 75–187 μ ; oral sucker

60–90 μ ; pharynx 22 μ ; ventral sucker 30–37 μ ; holdfast 52–60 μ ; reproductive fundament not seen (Hughes, 1927).

Final host: Alcedinidae (kingfishers)—*Ceryle alcyon*. United States.

9. *Neascus brevicaudatus* (von Nordmann, 1832), Diesing, 1850.

Fish host: In eyes of *Perca* and *Lota*; rare; not encysted (Zandt, 1924). Europe.

The author has recovered *Ornithodiplostomum ptychocheilus* metacercariae from the eyes of heavily infected experimental fish which were enclosed by the cyst of parasite origin only; in most instances this cyst ruptured so easily that the worms appeared unencysted.

Cyst: None.

Metacercaria: Forebody distinctly heart-shaped, narrowed posteriorly; ventral sucker smaller than oral sucker.

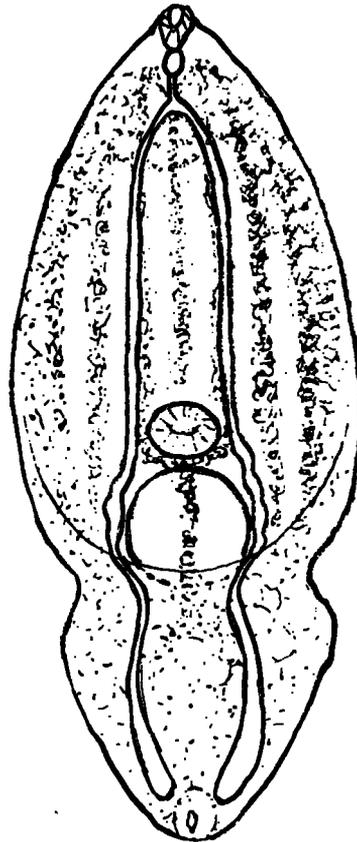


FIGURE 29.—*Neascus ellipticus* (from Chandler, 1951).

10. *Neascus ellipticus* Chandler, 1951.

Fish host: In musculature of *Perca flavescens*; cyst not pigmented. Minnesota.

Cyst: Elongate, elliptical, almost transparent, not pigmented, 735–900 by 360–500 μ ; parasite does not nearly fill the cyst.

Metacercaria (fig. 29): Two distinct body regions; forebody thin, shaped like a shallow spoon 450–540 by 300–325 μ (stretched–750 μ); hindbody 240–290 by 250–290 μ with posterior end rather pointed; oral sucker 30–42 by 22–30 μ ; no prepharynx; pharynx 25–35 by 17–20 μ ; short esophagus; ventral sucker 46–55 by 55–63 μ ; holdfast 100–125 μ ; reserve excretory system resembles that of *P. minimum* (*Neascus vancleavei*) (Chandler, 1951).

11. *Neascus* of *Cercaria flexicorpa* Hobgood, 1938.

Very similar to *Neascus* of *Uvulifer ambloplitis*. Oklahoma.

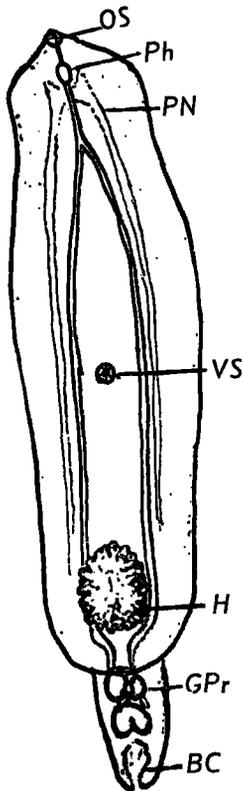
12. *Neascus grandis* Mueller and Van Cleave, 1932.

FIGURE 30.—*Neascus grandis* (from Mueller and Van Cleave, 1932).

Fish host: In viscera of *Umbra limi*. Resembles *Posthodiplostomum prosostomum* adult (Mueller and Van Cleave, 1932). New York.

Cyst: No description.

Metacercaria (fig. 30): Forebody much elongated, 1,500 by 360 μ ; hindbody 240 by 150 μ ; oral sucker ca. 22 μ ; pharynx 47 μ long; esophagus 105 μ ; ventral sucker 35 μ ; holdfast 170 by 120 μ ; holdfast gland indistinct or wanting; genital primordium large (Mueller and Van Cleave, 1932).

13. *Neascus longicollis* Chandler, 1951.

Fish host: In integument of *Perca flavescens*. Minnesota.

Cyst: Oval, pigmented, 480–640 by 450–500 μ , thickness 35–65 μ ; parasite not nearly filling cyst.

Metacercaria (fig. 31): Forebody 600–700 by 235–260 μ ; hindbody tail-like and narrower near forebody 170–270 by 60–120 μ ; anterior end of forebody terminating in a mobile finger-like process; oral sucker 38–42 μ ; no pharynx; ventral sucker 30 by 33–35 μ ; holdfast 100–110 μ ; reserve excretory system similar to *Neascus ambloplitis* group.

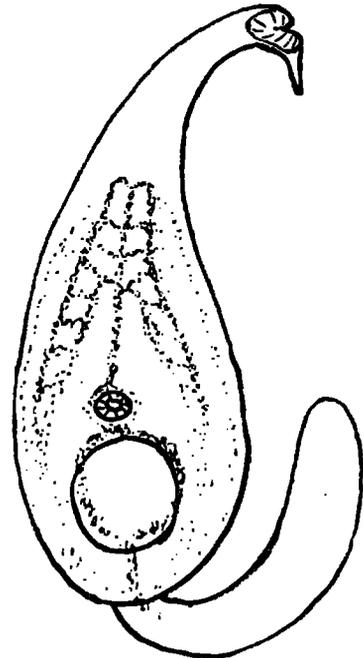


FIGURE 31.—*Neascus longicollis* (from Chandler, 1951).

14. *Neascus musclicola* (Waldenburg, 1860).
 Fish host: In integument and musculature of *Perca*, *Scardinius*, *Abramis*, and *Leuciscus*. Europe.
 Cyst: Not pigmented.
 Metacercaria: Similar to *Neascus cuticola* but the body is smaller, not folded in cyst, and hindbody is relatively larger.
15. *Neascus nolfi* Hoffman, 1955.
 Fish host: In integument and musculature of *Semotilus* and *Notropis* (Hoffman, 1955a). North Dakota.
 Host cyst: Spherical, pigmented, 472–576 μ in diameter.
 Parasite cyst: 202–324 μ ; cannot be easily separated from host cyst although parasite is relatively easily freed.
 Metacercaria (fig. 32): Two distinct body regions; body 229–382 by 137–153 μ ; great

width of forebody striking; forebody 229 by 147 μ ; hindbody 61–107 by 52–61 μ ; oral sucker 41 by 44 μ ; no prepharynx; pharynx 13 by 12 μ ; esophagus 24–27 μ long; ventral sucker 17 μ ; holdfast 55 μ ; reserve excretory system not discernible.

16. *Neascus pyriformis* Chandler, 1951.
 Fish host: In integument of *Perca flavescens*. Minnesota.
 Host cyst: pigmented, spherical to ovoid, 400–550 by 300–540 μ , 10–65 μ thick.
 Parasite cyst: Pear-shaped, 225–319 by 130–195 μ ca. 7–8 μ thick; difficult to free larva; parasite almost completely filling cyst.
 Metacercaria (fig. 33): Forebody 435–465 by 240–255 μ ; hindbody 150–250 by 125–175 μ ; oral sucker 70 by 45 μ ; pharynx difficult to see, 21–23 by 17–18 μ ; caeca not seen; ventral sucker 38–45 by 38–40 μ ; holdfast 85–105 by 80–95 μ ; reserve bladder similar to *N. ambloplitis* group (Chandler, 1951).

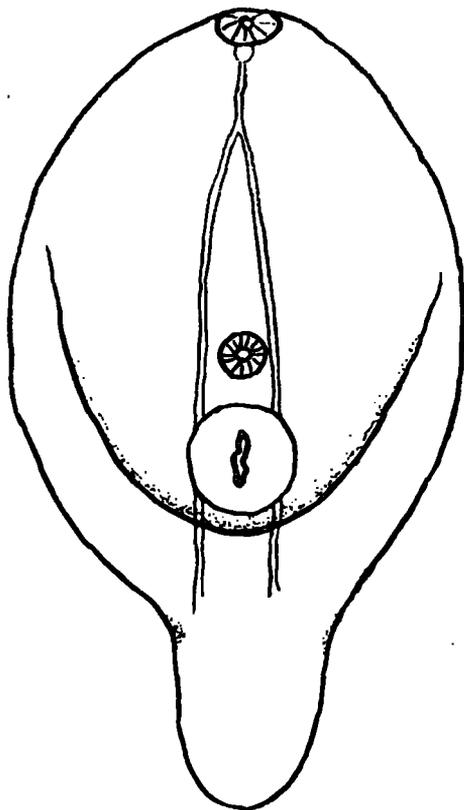


FIGURE 32.—*Neascus nolfi* (from Hoffman, 1955a).

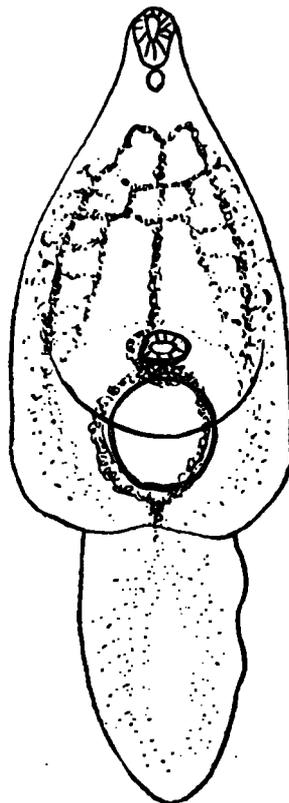


FIGURE 33.—*Neascus pyriformis* (from Chandler, 1951).

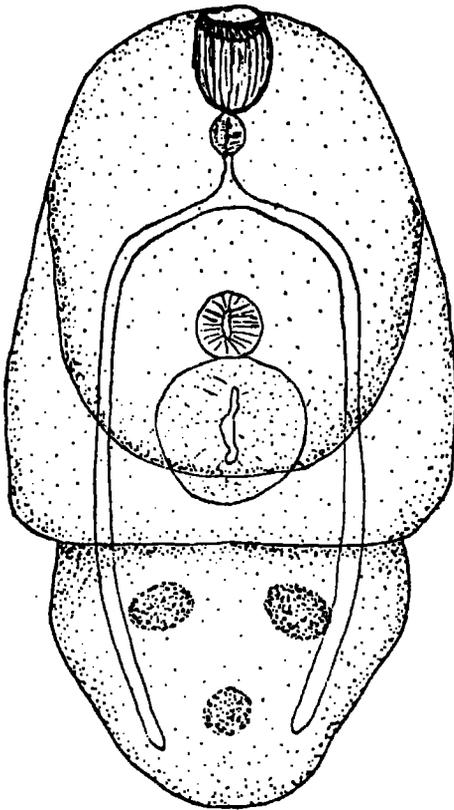


FIGURE 34.—*Neascus rhinichthysi* (from Hunter, Wanda, 1933). [This is probably from a contracted specimen.]

17. *Neascus rhinichthysi* Hunter, 1933.

Fish host: In integument of *Rhinichthys* species; New York.

Host cyst: Spherical, pigmented, 480–880 μ .

Parasite cyst: Nearly spherical, 223–380 μ ; larva nearly fills cyst and is easily freed.

Metacercaria (fig. 34): Two distinct body regions; forebody 232–301 by 135–194 μ ; hindbody 97–203 by 120–135 μ ; oral sucker 54–63 by 48–77 μ ; pharynx about 20 μ wide; ventral sucker 31–39 μ ; holdfast 69–81 μ ; genital primordia present; reserve bladder similar to *N. ambloplitis* (Hunter, W., 1933).

18. *Neascus wardi* Hunter, 1928.

Fish host: Encysted in *Lepomis cyanellus*. Illinois.

Host cyst: Pigmented, elliptical, 510–850 μ long.

Parasite cyst: Ovoid, tough but flexible, 300–400 μ long.

Metacercaria: Body 378–817 by 95–351 μ ; two distinct body regions; forebody 196–473 long; hindbody 115–419 by 41–236 μ ; oral sucker 40–79 μ ; pharynx 20–25 by 16–20 μ ; esophagus 10–15 μ long; ventral sucker 22–43 μ ; holdfast 40–79 μ ; three bodies in forebody believed to be genital primordia (?); reserve excretory system similar to *N. ambloplitis* [fixed specimens (Hunter, Wanda, 1928)]; Van Cleave and Mueller (1934) state that this form is probably identical with *N. ambloplitis*.

KEY TO THE KNOWN SPECIES OF NEASCUS OF NORTH AMERICAN FRESHWATER FISH

Key extracted and slightly modified from Hoffman (1955). Undoubtedly there are many other undescribed species of *Neascus*.

1. In cranial cavity of *Notropis cornutus frontalis* and *Pimephales p. promelas*; small oval cyst; adult in chick (experimental) (Hoffman, 1954)..... *Ornithodiplostomum pychocheilus* 2
1. In viscera, mesenteries, peritoneum..... 2
1. In musculature and integument..... 4
2. Relatively short hindbody; constriction slight; relatively small (cyst 750 μ); in mesenteries of Cyprinidae; adult in mergansers, squaw duck, and experimental in domestic duck and unfed chick (Hughes and Piszczek, 1928; Van Haitsma, 1930; Hoffman, 1954)..... *Ornithodiplostomum pychocheilus*
2. Relatively large hindbody; constriction pronounced; much larger (metacercaria more than 1 mm.); adults in herons, experimental in unfed chicks..... *Neascus of Posthodiplostomum spp.* 3
3. In liver, kidneys, and on heart of centrarchids (Ferguson, 1943, Hoffman, 1958; Hughes, 1928b; Van Cleave and Mueller, 1934: 249)..... *P. minimum centrarchi*
3. In mesenteries of cyprinids (Hughes, 1928b; Hoffman, 1958)..... *P. m. minimum*
3. In mesenteries of *Umbra limi*; forebody very large; ventral sucker in center of forebody; adult unknown (Mueller and Van Cleave, 1932: 93)..... *Neascus (Posthodiplostomum?) grandis*
4. Black pigment surrounding cyst;¹ resembles *P. minimum* somewhat..... 5
4. No black pigment surrounding cyst..... *Neascus ellipticus*
5. Metacercaria nearly fills the parasite cyst..... 6
5. Metacercaria does not fill the parasite cyst..... 9
6. Parasite cyst pyriform..... 7
6. Parasite cyst oval or round..... 8
7. Parasite cyst about 330 by 200 μ ; in many fish; adult in kingfisher (Hughes, 1927)..... *Uvulifer ambloplitis*
7. Parasite cyst smaller (about 270 by 160 μ), abruptly narrowed at one end; in perch; adult not demonstrated, possibly is *Uvulifer semicircuncisus* in kingfisher (Chandler, 1951)..... *Neascus pyriformis*
8. No ventral sucker; reserve excretory system similar to that of *N. ambloplitis* but forebody greatly cup-shaped (Hughes, 1928c)..... *Crassiphiala bulboglossa*
8. Ventral sucker present; reserve excretory system similar to *N. ambloplitis* although simpler; in dace; adult unknown (Hunter, Wanda, 1933)..... *Neascus rhinichthysi*
9. Smaller (parasite 200 to 330 μ); reserve excretory system indistinct; in *Semotilus a. atromaculatus*, *Notropis cornutus frontalis*, possibly others; adult unknown (Hoffman, 1955a)..... *Neascus nolli*
9. Quite large (parasite cyst 450 μ long, metacercaria 870 μ long); metacercaria with finger-like anterior papilla; in perch; adult unknown (Chandler, 1951)..... *Neascus longicollis*

IV. PROHEMISTOMULUM

This larval group has been described by Ciurea (1933) and possesses these characteristics: (1) body round or oval, flat, and foliaceous, not separated into two parts, (2) no lateral pseudosuckers, (3) hold-fast well developed, (4) reserve excretory system (bladder) consisting of two main vessels, one lateral and the other median, containing small calcareous corpuscles. Peripheral vessels bifurcate anteriorly giving rise to the median which also connects with it at the posterior extremity.

The nature of the reserve excretory system is very helpful for separating some *Prohemistomulum* species from some *Neascus* species which have indistinct hindbodies. The author's interpretation of the system of an undescribed species of cyathocotyloid metacercaria is here offered as an addition to the larval group description: (4) reserve excretory system consisting of three broad vessels, continuous and looped in such a fashion as to form a crude letter "W," and fusing anteriorly in many anastomoses, and containing calcareous corpuscles throughout (fig. 35).

¹ Sometimes the pigment does not appear until 2-3 weeks after infection.

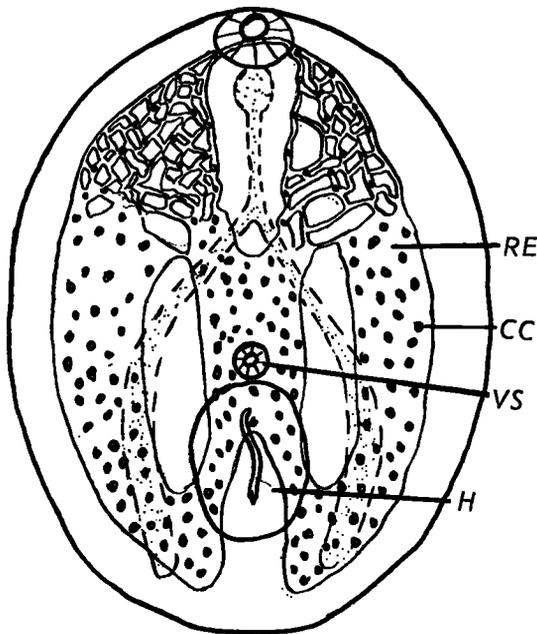


FIGURE 35.—Prohemistomulum (*cyathocotyliid*) metacercaria showing "W" form of the excretory bladder.

A. Family CYATHOCOTYLIDAE Poche, 1926.

1. *Cyathocotyle gravieri* Mathias, 1935.

Snail host: *Bithynia tentaculata*.

Fish hosts: Cyprinidae—Goujons (*Gobio*) and varions (*Phoxinus*), both experimental; encysted in the musculature.

Cyst: Ovoid, wall very thick; 500 by 300 μ .

Final host: Anatidae (ducks)—*Anas platyrhynchos domestica* (experimental).
France.

2. *Cyathocotyle melanittae* Yamaguti, 1934.

Snail host and cercaria unknown.

Fish host: Cyprinidae—*Pseudorasbora parva*; encysted in the musculature.

Cyst: Spherical to elliptical, 198–250 by 150–250 μ ; consisting of 5 layers.

Metacercaria: Body 140–160 by 140–156 μ , minutely spined; oral sucker 45–50 μ wide (wider than long); pharynx 18–20 μ ; esophagus short; no. ventral sucker; holdfast 80–199 μ in diameter; genital primordium not seen (Yamaguti, 1942).

Final host: *Melanitta fusca*; ducklings; experimental (Yamaguti, 1942). Japan.

3. *Cyathocotyle orientalis* Faust, 1921.

Snail host: *Bulinus striatulus japonicus*.

Fish host: Cyprinidae—*Pseudorasbora parva*.
Family (?)—*Sorcocheilichthys sinensis*.
Encysted in muscle and connective tissue.

Cyst and metacercaria: Descriptions controversial. Faust (1921) described the metacercaria as a *Tetracotyle*, but this must be an error. Yamaguti's photograph of the encysted metacercaria, however, clearly shows the cyathocotyliid type of reserve excretory system.

Final host: Anatidae—domestic mallard (experimental). Falconidae: *Milvus migrans lineatus* (kite). Japan (Yamaguti, 1940).
Description not detailed enough for comparison with Faust (1921), therefore, the author is not sure that they are identical.

4. *Holostephanus ictaluri* Vernberg, 1952.

Final host: Siluridae—*Ictalurus punctatus*.
Intestine.

5. *Linstowiella szidati* (Anderson) Anderson and Cable, 1950.

Snail host: *Campeloma rufum*.

Fish host: Cyprinidae—*Notropis cornutus*; encysted in the musculature.

Cyst: Nearly spherical, 400 by 300 μ ; difficult to remove parasite from inner cyst; peptic and tryptic digests released worms but killed them.

Metacercaria: Not described, apparently similar to immature adults.

Final host: Young chick (experimental).
United States. (Anderson and Cable, 1950).

6. *Mesostephanus appendiculatoides* (Price, 1934) Lutz, 1935.

Snail host: marine snail, *Cerithium muscarum*.

Fish host: Mugilidae—*Mugil* species.

Cyst: 300–381 by 327–411 μ . Description not available to author; encysted in the musculature and pericardial wall.

Final hosts: *Didelphis virginiana* (opossum); *Procyon lotor* (raccoon); *Larus delawarensis* (ring-billed gull); *Nyctocorax n. hoactli* (black-crowned night heron) (experimental); *Pelecanus occidentalis* (Hutton and Sogandares-Bernal, 1959).

7. *Mesostephanus appendiculatus* (Ciurea, 1916)
Lutz, 1935.

Snail host and cercaria unknown.

Fish host: Cyprinidae—*Abramis blicca*, *Carassius carassius*, *Tinca tinca*, *Aspius aspius*.

Cyst: Description not available to author.

Final hosts: Dog and cat (experimental); cat and dog (Kuntz and Chandler, 1956). Egypt; Romania; Ukraine; United States.

8. *Mesostephanus odhneri* (Travassos, 1924)
Lutz, 1935.

Snail host and cercaria unknown.

Fish host: Haemulidae (Perciformes)—*Haemulon* species; encysted beneath the skin.

Cyst: About 340 μ in diameter.

Metacercaria: 300 by 190 μ ; oral sucker 30 μ ; pharynx 20 by 14 μ ; ventral sucker 18–20 μ ; holdfast 80 by 60 μ .

Final host: Ardeidae (herons): *Nyctanassa violacea* (experimental). Brazil.

9. *Paracoenogonimus ovatus* Katsurada, 1914.
Snail host: *Viviparus viviparus*.

Fish host: Cyprinidae—*Abramis* species, *Cyprinus carpio*, *Idus idus*, *Leuciscus rutilus*, *Scardinius erythrophthalmus*, *Tinca tinca*. Esocidae—*Esox lucius*. Encysted in the musculature. See *Prohemistomulum circulare* (fig. 37).

Final host: Mice (experimental). Europe (Komiya, 1938).

10. *Prohemistomum chandleri* Vernberg, 1952.

Snail host: *Pleurocera acuta*; Cercaria of *Prohemistomum chandleri*.

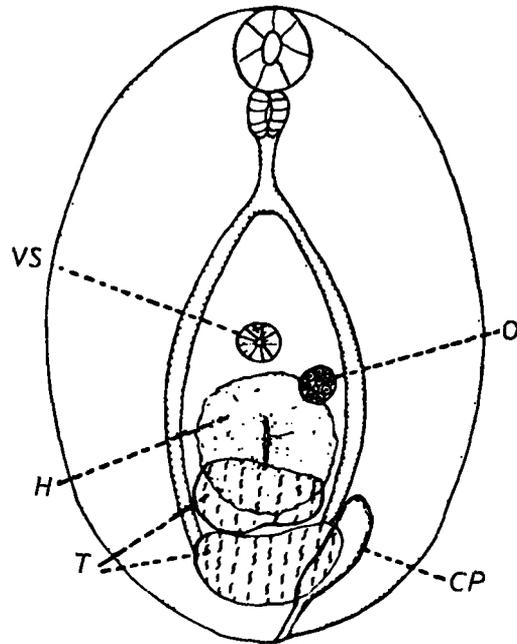


FIGURE 36.—*Prohemistomum chandleri*; adult. Prohemistomulum metacercaria not figured in original description. [The author assumes that the larval form is similar to that of the adult, but that the gonads are smaller or not yet formed (from Vernberg, 1952)].

Fish host: Centrarchidae—*Micropterus salmoides*, *M. dolomieu*.

Cyst: Spherical, pigmented, 606 by 475 μ average; space between host cyst and parasite cyst filled with granular material.

Metacercaria (fig. 36): Not described, apparently similar to immature adult.

Final hosts: Siluridae—*Ictalurus punctatus* (experimental adult). Cottidae—*Cottus bairdii* (experimental adult). Snake, *Matrix sipedon* (experimental adult). United States (Vernberg, 1952).

11. *Prohemistomum vivax* (Sonsino, 1892) Azim, 1933.

Snail host: *Cleopatra bulimoides*. Cercaria *Prohemistomum vivax* (Sonsino) Looss, 1896.

Fish hosts: Poeciliidae—*Gambusia affinis*. Cichlidae—*Tilapia nilotica*. Encysted in the muscles and peritoneal cavity [*Prohemistomulum vivax* (Sonsino) Azim, 1933].

Cyst: Spherical, pigmented, 300–320 μ in diameter, cf. Dubois (1938, p. 455).

Metacercaria: Description not available to author.

Final hosts: *Milvus*. Dog, cat. Egypt.

12. *Prosostephanus industrius* (Tubangui, 1922), Lutz, 1935.

Snail host: *Parafossarulus* species.

Fish host: Cyprinidae: Crucian carp.

Cyst: Description not available to author.

Final host: Experimental in cats (Tang, 1941). China.

13. *Szidatia joyeuxii* (Hughes, 1929) Dubois, 1938.

Snail host: *Melanopsis* species. [*Cercaria vivax* (Sons, 1894); *Cercaria s. joyeuxii* Balozet, 1953].

Fish hosts: Poeciliidae—*Gambusia affinis* (experimental), encysted in the musculature. Also in toad and frog.

Cyst: Spherical, white becoming black, 450–500 μ in diameter.

Metacercaria: 700 to 1000 by 450–550 μ ; oral sucker 60–70 μ ; ventral sucker 40–60 μ ; holdfast 175–230 μ long.

Final host: Snakes, *Malpolon*, and *Tropidonotus* species. Tunisia (Balozet, 1953; Joyeux and Baer, 1941).

B. Family undetermined, probably CYATHOCOTYLIDAE.

14. *Prohemistomulum circulare* Ciurea, 1933. [Perhaps is *P. ovatus*, cf. Dubois (1938): 452].

Fish host: Cyprinidae—*Abramis*, *Blicca*, *Cyprinus*, *Idus*, *Leuciscus*, *Scardinius*.
Esocidae—*Esox lucius*. Encysted in the musculature. Europe.

Cyst: Spherical to slightly ellipsoidal, 300–440 by 290–390 μ ; outer cyst wall 15–44 μ thick; inner cyst wall 6–13 μ thick.

Metacercaria (fig. 37): Oval, 280–360 by 190–230 μ ; oral sucker 46–57 μ ; pharynx 30–37 by 28–33 μ ; ventral sucker 22–33 μ ; holdfast 72–110 by 79–99 μ . Testes posterior to holdfast; ovary on left.

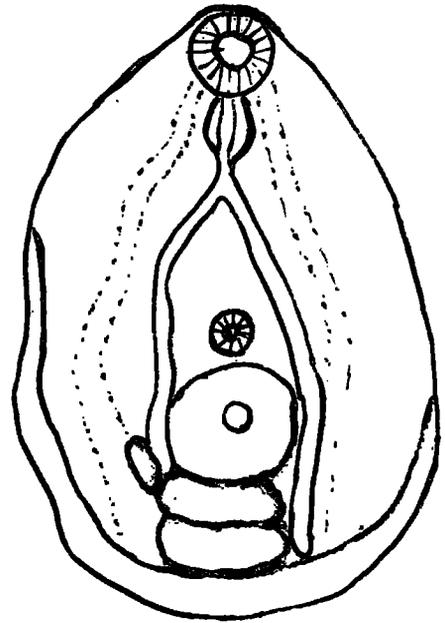


FIGURE 37.—*Prohemistomulum circulare* (from Ciurea, 1933).

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SONIC TRACKING OF ADULT SALMON AT BONNEVILLE DAM, 1957

BY JAMES H. JOHNSON



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ABSTRACT

Adult salmon bearing miniature sonic transmitters were tracked individually in the forebay of Bonneville Dam. Fish were tracked as far as 10 miles upstream and for periods ranging up to 16¼ hours. In the release area adjacent to the dam, the fish seldom swam more than 50 feet away from shore or remained away from it for more than 2 minutes at a time. After leaving the dam most fish followed the shoreline near which they were released; they rarely swam in water more than 30 feet deep. During daylight the average speed at which they traveled over the bottom was 1.5 miles per hour, and their net rate of movement upstream was 1.2 miles per hour. Each of the three fish tracked from daylight into darkness slowed its pace or ceased swimming as darkness deepened.

SONIC TRACKING OF ADULT SALMON AT BONNEVILLE DAM, 1957

By JAMES H. JOHNSON, *Fishery Research Biologist*
BUREAU OF COMMERCIAL FISHERIES

A more detailed knowledge of individual fish behavior in the immediate vicinity of dams is needed for the conservation of the Pacific Northwest salmon runs. Upstream migrants arriving at dams during periods of high river flow face serious delays in locating fishway entrances, or physical injury, or both, in the violent turbulence of spillway discharge. After a high flow period on the lower Columbia River in June 1955, large numbers of dead salmon were collected below Bonneville Dam by biologists of the Oregon Fish Commission. Exactly where and how these fish died is not known. But assuming that at least part of the mortality was the result of unsuccessful attempts to pass beyond the dam, the question arises whether it occurred primarily while the fish were seeking entrance to the ladders, or whether large numbers of fish were swept back through the spill gates after emerging from the ladders.

Knowledge of fish movements immediately above and below existing dams is meager. It was obtained largely from the estimated effective-

ness of various fish-collection systems and from visual observations limited by turbidity and hydraulic conditions. Conventional marking and tagging studies in the vicinity of dams provide average rates of movement from the release point to the point of recovery, but yield no information concerning fish movements between these points. As a method was clearly needed to overcome these limitations, special sonic equipment to track continuously the movements of individual fish was developed by the U.S. Fish and Wildlife Service. This equipment was first used to study the general behavior pattern of adult salmon in the forebay of Bonneville Dam.

During the late summer and fall of 1957, upstream migrants were tagged with sonic fish tags and their movements were precisely tracked in the Bonneville forebay. Individual fish were tracked as far as 10 miles upstream and for periods as long as 16½ hours. Although we have been limited thus far to working above the dam and under reduced river flow conditions (see fig. 1), we

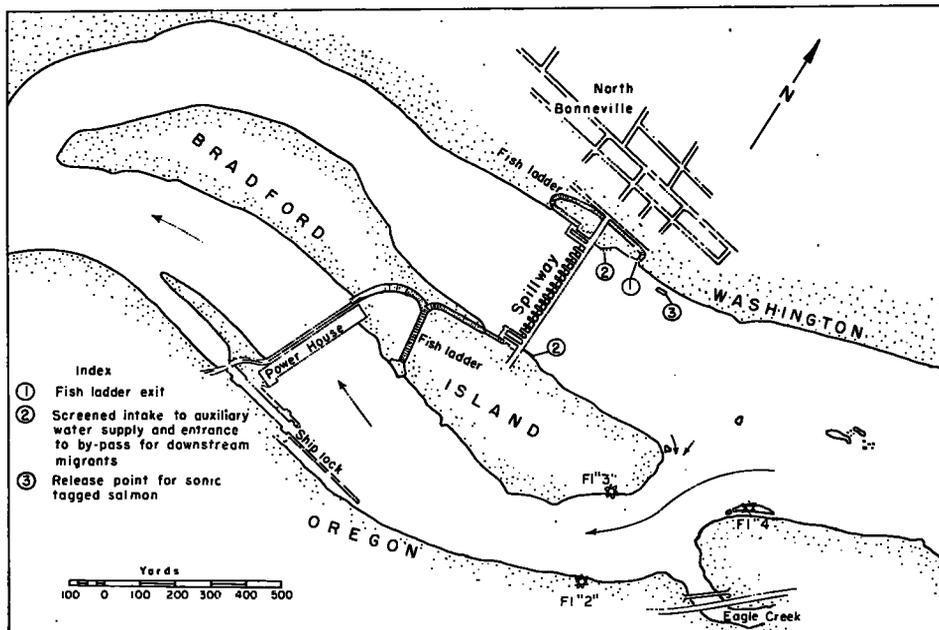


FIGURE 1.—Bonneville Dam. Fish were tracked during late August, September, and October, while the spillway was closed and the river flow was channeled entirely through the powerhouse.

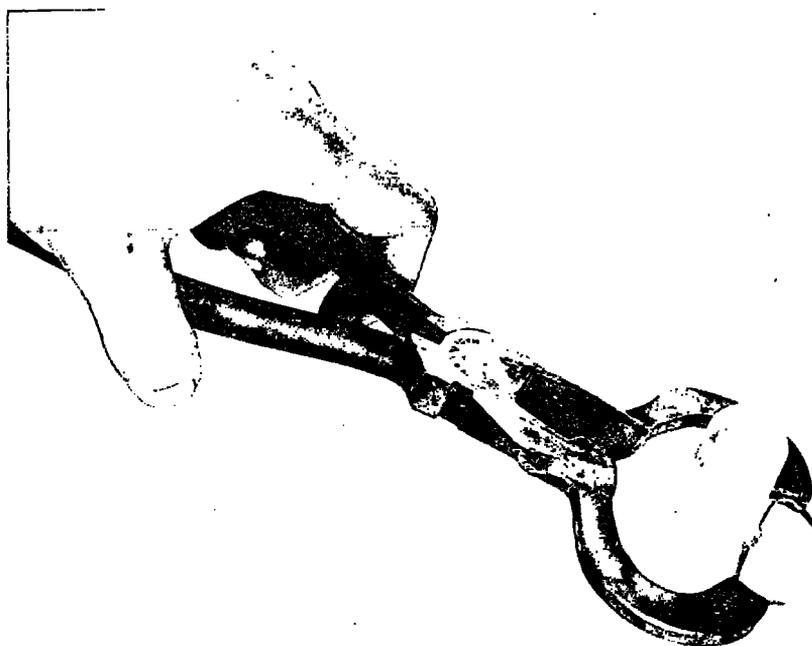


FIGURE 2.—Sonic tag held with tool used to attach the tag to the fish. The tag is activated prior to being used by twisting two protruding wires together.

believe the data presented will, with further observations obtained by the same method, contribute appreciably to our knowledge of fish behavior at dams.

We wish to thank the U.S. Army Corps of Engineers, Portland (Oregon) District, for permission to work in the vicinity of Bonneville Dam, and the Oregon Fish Commission for their assistance in trapping the fish.

This study was directed by Parker S. Trefethen and Dr. Gerald B. Collins of the Fish and Wildlife Service, Seattle Biological Laboratory; tracking was performed by John R. Pugh, John C. Mason, and the author.

MATERIALS AND METHODS

Equipment

Sonic equipment used to track individual fish includes a sonic tag and a special receiver mounted in a boat. The sonic tag, attached to a fish, transmits sound waves which are picked up by the receiver; an observer may thus record the position of the fish in relation to the boat.

The transmitter is contained in a thin aluminum capsule approximately 2.5 inches long and 0.9 inches in diameter (fig. 2). Soldered to each cap-

sule is a nickel-chromium wire "hog-ring" with sharp points for attaching the tag to a fish. The capsule contains battery-powered miniature electronic components, forming a transistorized oscillator which drives a resonating crystal cemented in one end of the capsule. Electronic components and capsule, coated with waterproof plastic, plus the attaching device, have a combined weight of 0 to 2 grams when immersed in water. Operating on a carrier frequency of 132,000 cycles per second with a pulsing rate of 1,000 to 2,000 cps., the tag transmits ultrasonic sound waves in all directions through the water with a usable range up to 800 feet. The expected life of the sonic tag used at Bonneville was 8 hours, although some lasted much longer.

The signal from the tag (fig. 3) is picked up by a receiver tuned to the tag's frequency. This unit is incorporated with an echo-ranging system (a modified Minneapolis-Honeywell Regulator Company "Sea-Scanar") to form an instrument which automatically tracks the sonic tag and indicates its position in relation to the receiver. The sonic-tagged fish appears as a "blip" of light on a cathode-ray tube viewing screen, calibrated to give direct readings of the bearing and distance of the

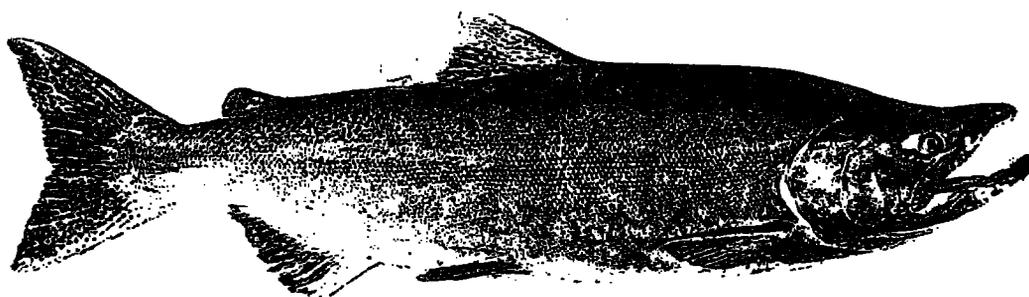


FIGURE 3.—Sonic tag attached to adult chinook salmon.

fish from the receiver. A tilt-angle meter which shows the vertical angle at which the signal is being received from beneath the surface makes it possible to calculate the depth at which the fish is swimming. More detailed descriptions of the sonic equipment are given by Trefethen (1956), and by Trefethen, Dudley, and Smith (1957).

At Bonneville the automatic receiver was mounted in an 18-foot boat (fig. 4). The equipment was powered by a 110 volt a.c. gasoline generator.

Tagging and tracking procedure

Fish were obtained from the Washington-shore fish ladder at Bonneville Dam. As the fish emerged from the ladder, they swam into a large floating trap operated by employees of the Oregon Fish Commission engaged in a separate tagging program. This trap was towed 100 yards upstream to a raft which was anchored 50 feet offshore. A single fish was quickly transferred by

dipnet from the trap to a live box 4 feet long, 2 feet wide, and 2½ feet deep. Some fish were tagged immediately; others were held in the live box as long as 2 hours before tagging (table 1). Open at the top, the live box was raised until the back of the fish was approximately an inch beneath the surface of the water. As soon as the fish momentarily stopped moving, with special pliers (fig. 2) a sonic tag was fastened in place behind the dorsal fin (fig. 3). The lid was then fastened shut and the live box completely submerged. After an additional holding period of approximately 20 minutes a vertical slide gate in one end of the live box was raised and the fish was free to swim out.

Our crew waited 50 to 75 feet away in the boat with the tracking gear in operation, ready to follow the fish up or down stream as it emerged from the live box. Each fish was tracked until we lost the

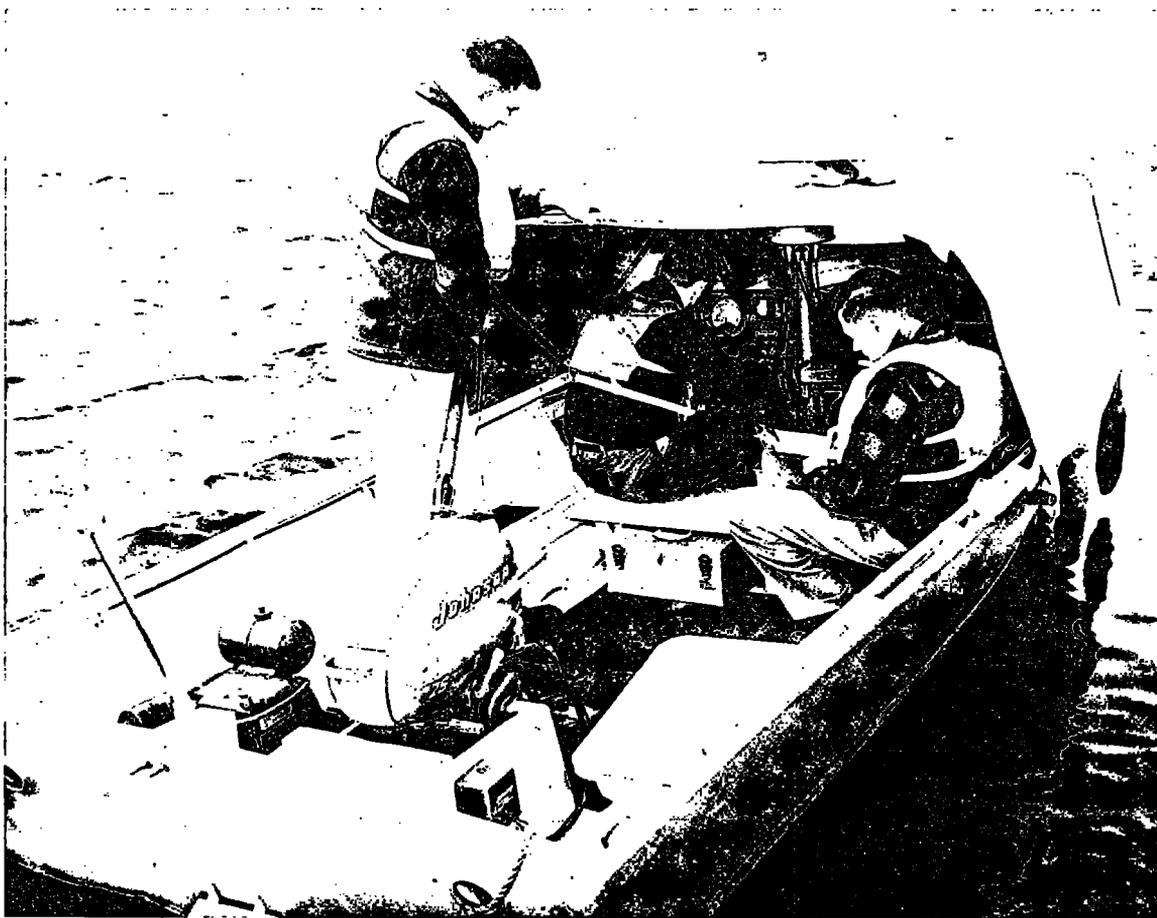


FIGURE 4.—Sonic equipment and crew in position aboard the fish-tracking boat.

signal, and an additional hour usually was spent searching the area, trying to reestablish contact. Sufficient supplies were carried each day to operate for periods up to 20 hours if necessary.

A three-man crew was required to operate the equipment and record the observations. Their duties were as follows: One man operated the boat and tended the power supply for the sonic equipment; a second operated the sonic equipment and signaled instructions to the boat operator to keep the tagged fish within range; the third recorded data on the location of the fish as determined by the sonic gear operator, and also maintained a log of the position of the boat. This was done by descriptive notation (e.g., "time 1232—beneath Bridge of the Gods, 30 feet off Washington shore") and by taking cross-bearings with a sighting compass on river navigation markers, land points, islands, bridges, and other fixed landmarks along shore.

RESULTS

Fish movements in the release area

Of the 43 fish tagged and released, 37 were fall run chinook salmon (*Oncorhynchus tshawytscha*); the 2 silver salmon (*O. kisutch*) and 4 steelhead trout (*Salmo gairdnerii*) listed in tables 1 and 2 were tagged on days when chinooks were unobtainable.

We considered the release area to be that part of the forebay which extends 500 yards above the spillway. The area is bordered on the north side by the Washington shore and on the south by Bradford Island. Safety regulations did not permit our boat to approach closer than 300 yards to the dam until flow through the spillway was reduced to approximately 15,000 cubic feet per second. This condition channels the river flow almost entirely down the south side of Bradford Island through the powerhouse and leaves the forebay area for a quarter of a mile above the

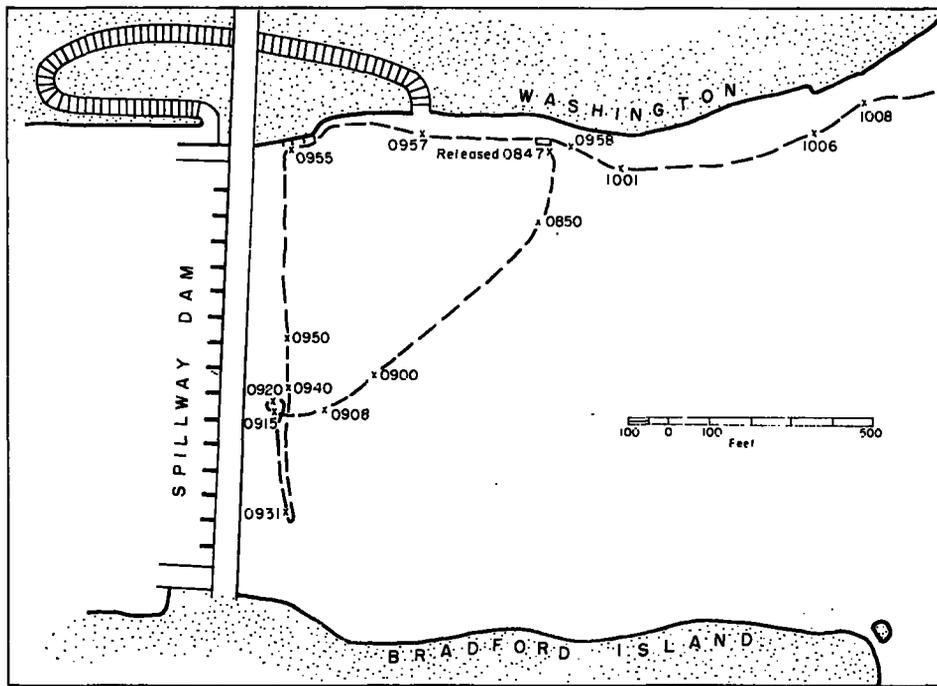


FIGURE 5.—Movements in release area of fish tracked on September 3, 1957, in Bonneville Dam forebay (see also fig. 10).

spillway relatively free of strong currents. From August 23 until observations were completed, all (18) of the main spill gates were completely closed. The only remaining flow through the release area was that drawn off by the Washington-shore fish ladder (about 200 cfs.) and by 2 screened fishway auxiliary water-supply intakes (fig. 1). Current velocity at these 3 points was less than 2 feet per second and decreased to near zero within a few yards outside of the intakes. During this period, after August 23, the general area in which the fish were released resembled a lake more than a river.

The plots shown in figures 5, 6, and 7 are representative of movements of the fish which were observed in the release area. A fish tracked on September 8 (fig. 6) was typical in that it remained close to the Washington shore, repeatedly reversed its course up and downstream, and finally began to swim steadily upstream an hour after release.

Sixty-two percent of the fish swam no farther than 50 feet from the Washington shore while moving about within the release area. Fish that left the Washington shore usually kept close to the face of the spillway or Bradford Island or quickly returned to the Washington shore. Fish tracked

in the release area spent more than 90 percent of a total of 47 hours swimming within 50 feet of one of these three boundaries. With 5 exceptions fish did not spend more than 10 minutes at any one time away from shore and were seldom away from it as much as 2 minutes at a time.

The average swimming speed for these fish in deep water (0.9 m.p.h.) was almost twice as fast as near shore, with the added difference that offshore they moved continuously but inshore frequently stopped swimming.

Some fish moved out of the release area in less than two minutes; others remained there as long as 4 hours and 50 minutes before moving out. One fish still remained in the area when contact was lost nearly 5 hours after release (table 1). The average time spent by fish in the release area was 1½ hours.

Suspecting this "move-out time" might be dependent on size of fish, or length of holding period, or both, we examined by multiple regression the contribution of these factors to the time the fish took between release from the live box and the beginning of sustained upstream movement. While the contribution of size was negligible, the contribution of time held was significant at the 10-percent level. Thus it appeared that fish held

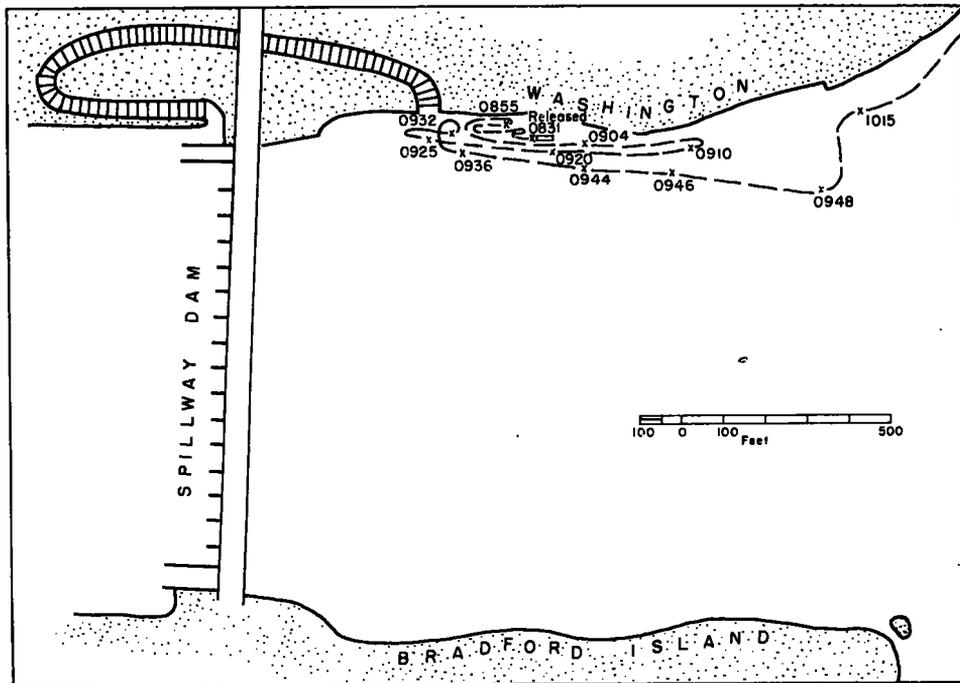


FIGURE 6.—Movements in release area of fish tracked on September 8, 1957, in Bonneville Dam forebay.

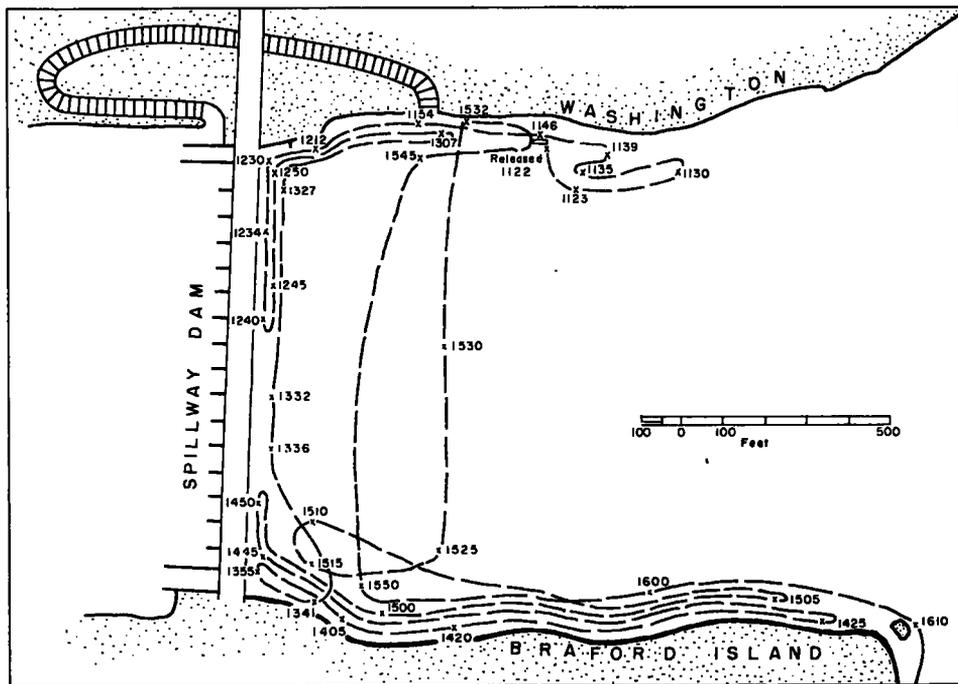


FIGURE 7.—Movements in release area of fish tracked on September 18, 1957, in Bonneville Dam forebay. Fish crossed powerhouse channel to Oregon shore and entered Eagle Creek.

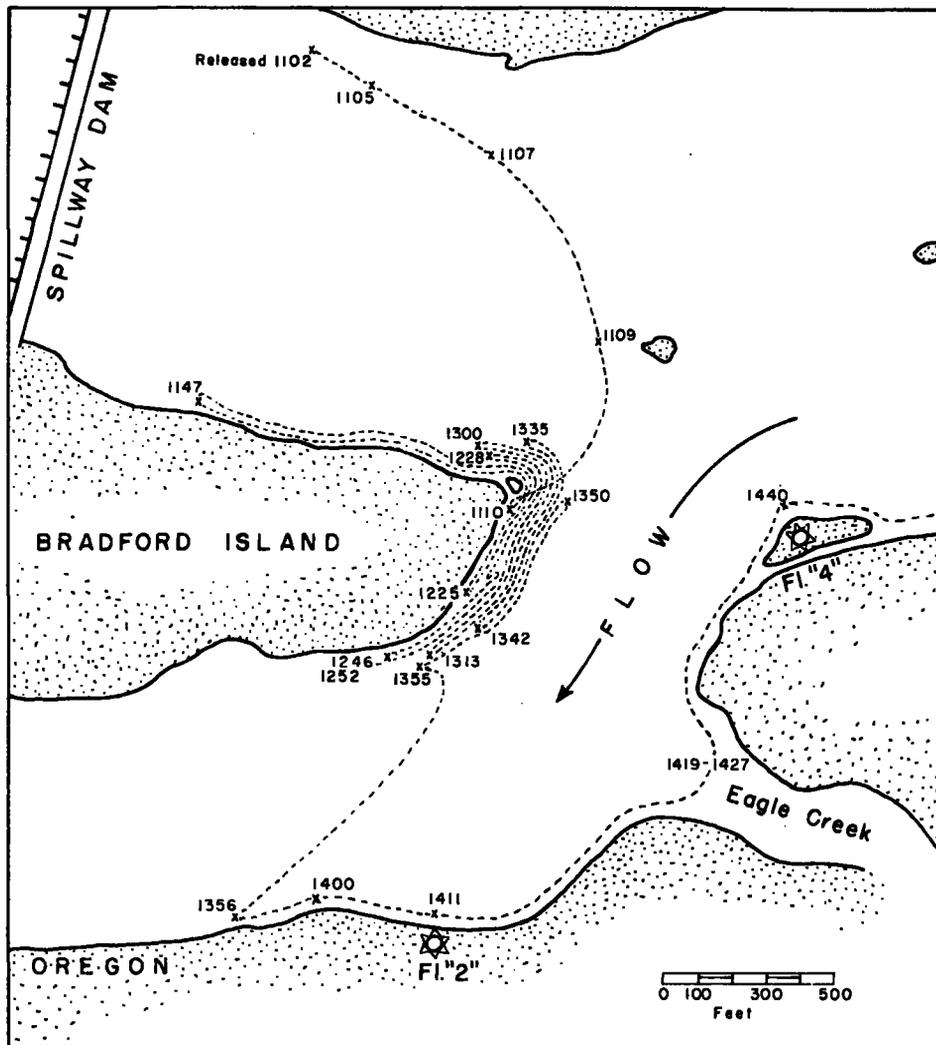


FIGURE 8.—Movements of fish tracked in the release area, forebay of Bonneville Dam, September 13, 1957 (see also fig. 12).

longer in the live box moved out of the release area sooner.

The fish tracked September 3 (figs. 5 and 10) was one of nine that swam downstream to within 50 feet or less of the spillway. Seventy percent of the fish tracked moved some distance downstream from the release point before returning upstream, or before contact with them was lost.

The fish tracked September 18 (fig. 7) made more crossings at the spillway ($3\frac{1}{2}$) and also traveled farther (2.8 miles) than any other fish before leaving the release area. The average distance traveled within the release area was slightly more than one-half mile. In this wandering prior to moving out, the fish did not appear to

show any particular interest in the three water-intake points (fig. 1). Occasionally a fish would pause for a minute or two in front of one of these screened intakes, but much more often swam past without slowing.

The performance of the fish tracked on September 13 (figs. 8 and 12) was especially interesting. Halfway across the spillway forebay it appeared to be heading directly toward the mouth of Eagle Creek on the Oregon side. As it came into the current above the tip of Bradford Island, however, it veered sharply to shore, then began to swim in a series of arcs around the tip of the island. The plot in figure 8 is diagrammatic in that the fish actually maintained

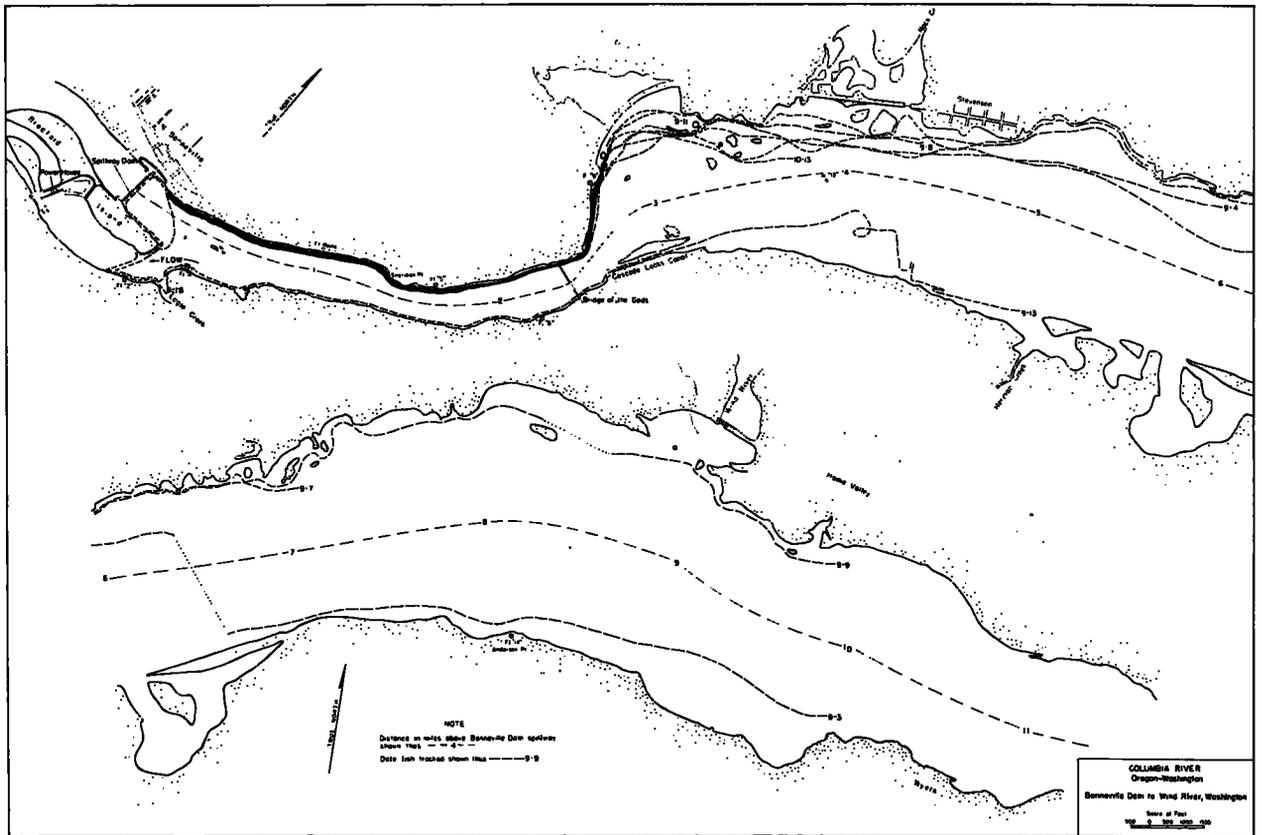


FIGURE 9.—Composite plot of 23 fish tracked out of release area, Bonneville Dam, 1957.

a constant distance, 15 to 30 feet offshore on the current side of the island and 40 to 60 feet offshore on the spillway side, from the time it arrived at the island until it departed, except for six or seven traverses when it ventured as much as 50 feet into the current, but returned quickly each time. These abortive dashes offshore made it appear that the fish was eager to continue upstream but perhaps reluctant to leave the reference point provided by the island shoreline. When it finally did break away it swam or drifted more than 500 feet downstream with the current before arriving at the Oregon shore. It immediately began moving upstream, again keeping within 20 feet of the shoreline.

We were able only intermittently to obtain readings of the exact distance of fish from the boat, and so were seldom able to calculate their exact depth. In water less than 30 feet deep along shore where the fish generally stayed, the instrument readings frequently indicated that fish were swimming so close to the bottom as to blend into

the echo, and thus failed to return a distinguishable blip on the cathode-ray-tube viewing screen. The blips we recorded, representing 22 fish, placed them at all depths from surface to bottom.

Farther offshore, in water as deep as 100 feet, the 8 fish on which positive blips were recorded were seen most frequently between 5 and 25 feet beneath the surface; 40 feet was the greatest depth at which any fish was seen. Some may have been lost by descending deeper. The sonic tag was unable to withstand pressures encountered below approximately 50 feet. The tag now in use has a thicker wall capable of withstanding pressure at a depth of 200 feet. Tag failure due to leakage is the most likely explanation of the loss of contact with a number of fish immediately following their release.

Fish movements above the release area

Twenty-three fish were tracked for some distance above the release area, and once they had left the area their movements became strikingly uniform. This is shown clearly in figure 9,



FIGURE 10.—Course of fish tracked September 3, 1957, Columbia River (Washington-Oregon), Bonneville Dam to Wind River, Washington.

Miles upstream from Bonneville Dam spillway indicated by: --- 4 ---

Course of fish and hour of day (military time) indicated by: --- x ---

1035

particularly through the constricted 2-mile section of river between the release area and the Bridge of the Gods. Bottom contour lines superimposed on figure 9 would show that, having left the area, sonic-tagged fish seldom crossed over the 30-foot contour line into deeper water. Between the release area and the Bridge of the Gods, the bottom drops off sharply along both sides of the river, which may account for the fish usually traveling within 10 to 25 feet of shore as they swam through this section.

Above the Bridge of the Gods, fish that followed the Washington shore continued to swim close to the bank consistently until they had passed navigation marker F9. Here they came into extensive shallows (depths of less than 20 feet) for the first time since leaving the dam, and the routes of individual fish began to vary. However,

the general pattern continued—that of fish remaining within water not more than 30 feet deep.

The average rate of movement also remained nearly constant. The 9 fish tracked above the Bridge of the Gods averaged 1.51 m.p.h., from the release area to the bridge and 1.47 m.p.h., from that point. These averages are based on the total distance traveled over the bottom by each fish during hours of daylight. Calculated on a river-mileage basis (see figs. 9–14), the average net speed above the bridge decreases to 1.21 m.p.h. In the general course followed by fish along the Washington shore, current velocities also averaged slightly less above the Bridge of the Gods than below it. These velocities ranged from 2 feet per second to less than $\frac{1}{4}$ foot per second. We estimated the actual swimming speed of several fish (speed over the bottom plus speed of the opposing current) at 3.5 to 4.0 miles per

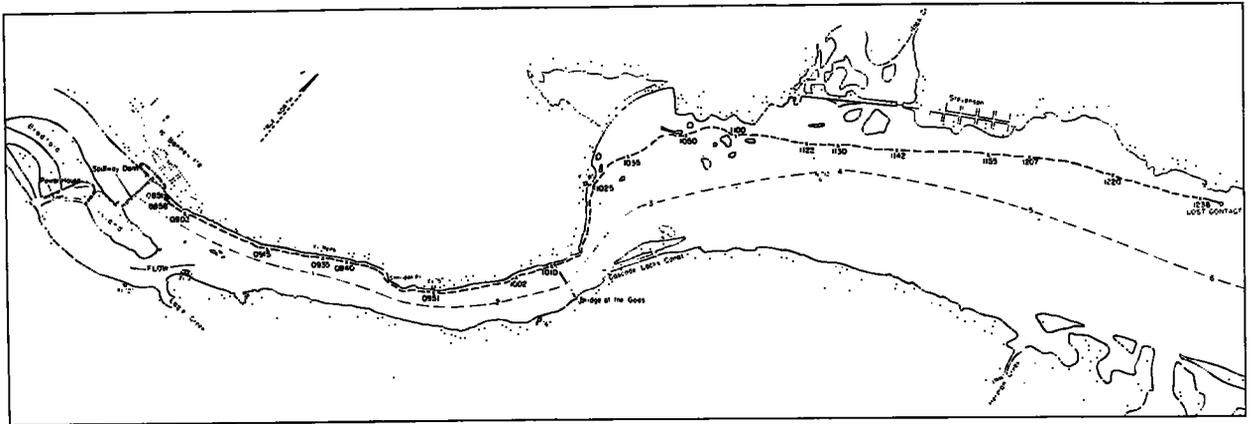


FIGURE 11.—Course of fish tracked September 4, 1957, Columbia River (Washington-Oregon), Bonneville Dam to Herman Creek, Oregon.

Miles upstream from Bonneville Dam spillway indicated by: -- 4 --
 Course of fish and hour of day (military time) indicated by: --- x ---

1010

hour for short distances while they were swimming against current velocities of $1\frac{1}{2}$ to 2 feet per second.

In traveling the 9 miles from Bonneville to Wind River, fish that followed the Washington shoreline traveled roughly a mile farther than if they had kept to deep water in midchannel, or $1\frac{1}{4}$ miles farther than they would have, had they followed the Oregon shore.

Three chinook salmon were tracked from daylight into darkness, and each evening as it grew dark the fish either slowed their pace or came to a complete halt. The comparative rates of movement were as follows:

Date	Before dark	After dark
1957		
	(M.p.h.)	(M.p.h.)
Sept. 9	1.29	0.42 (Fig. 14)
Sept. 13	0.86	.06 (Fig. 12)
Oct. 617	0

One fish tracked on September 9 (fig. 14) gradually slowed its pace until it was barely making headway. At the same time (1935 hours) it became necessary to use a flashlight in taking notes. A short time later, the fish stopped moving. One hour and 15 minutes later, the fish began to swim again, and on the final mile its

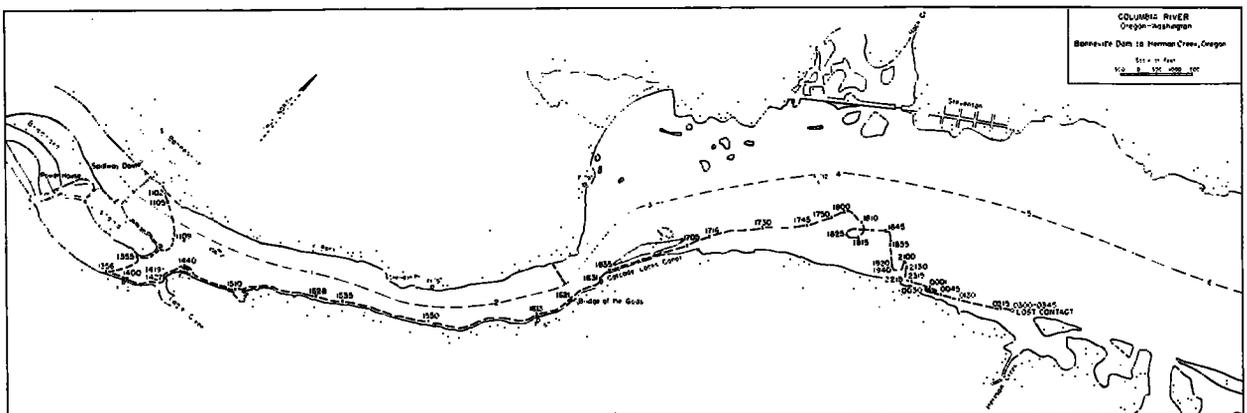


FIGURE 12.—Course of fish tracked September 13, 1957, Columbia River (Washington-Oregon), Bonneville Dam to Herman Creek, Oregon.

Miles upstream from Bonneville Dam spillway indicated by: -- 4 --
 Course of fish and hour of day (military time) indicated by: --- x ---

1550

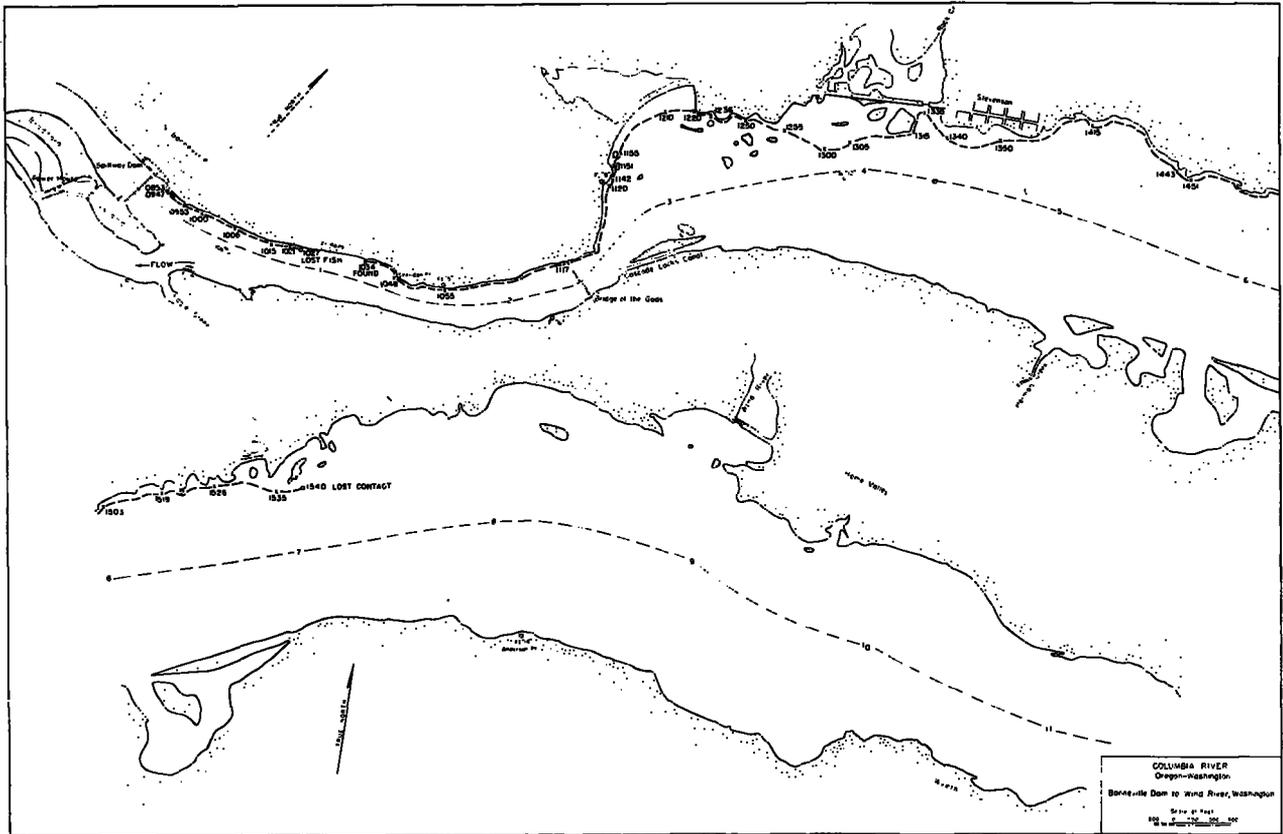


FIGURE 13.—Course of fish tracked September 7, 1957, Columbia River (Washington-Oregon), Bonneville Dam to Wind River, Washington.

Miles upstream from Bonneville Dam spillway indicated by: --- 4 ---

Course of fish and hour of day (military time) indicated by: --- x ---

1055

average speed was 1 mile per hour. The fish resumed upstream movement less than 5 minutes after the moon rose full from behind a mountain.

The net distance upstream traveled after dark by the September 13 fish (figs. 8, 12) was one-half mile. During the 8½ hours of darkness the fish alternated between moving up and downstream over short distances at a very slow rate of speed and remaining in one spot for periods ranging up to 1 hour. At times it moved neither up nor downstream, but moved slowly toward or away from shore.

Only one fish crossed the river above the release area (fig. 10). Contact with it was lost for 22 minutes and was not regained until some time after the fish had reached the Oregon shore. The other two fish that crossed to the Oregon side did so in the vicinity of the dam. One made its way sporadically 200 yards into Eagle Creek, stopped,

and was in the same spot 2½ hours later at dark, when it had to be abandoned (figs. 7 and 9). The fish tracked September 13 nosed into the mouth of Eagle Creek but left within 8 minutes. It was delayed 20 minutes more a short distance above the creek mouth by apparent reluctance to pass underneath or around a large river tow boat tied along shore with engines idling. Once past this it swam steadily upstream until it arrived at the old Cascade Locks ship canal, no longer in use since the completion of Bonneville Dam. The fish hesitated several minutes before entering this 100-foot wide concrete channel and once inside moved slowly the length of it, pausing frequently, and keeping mostly to the middle. Two dozen or more sport fishermen were fishing from the banks of the canal at the time.

Extending downstream from Sheridan Point over a distance of approximately one-half mile,

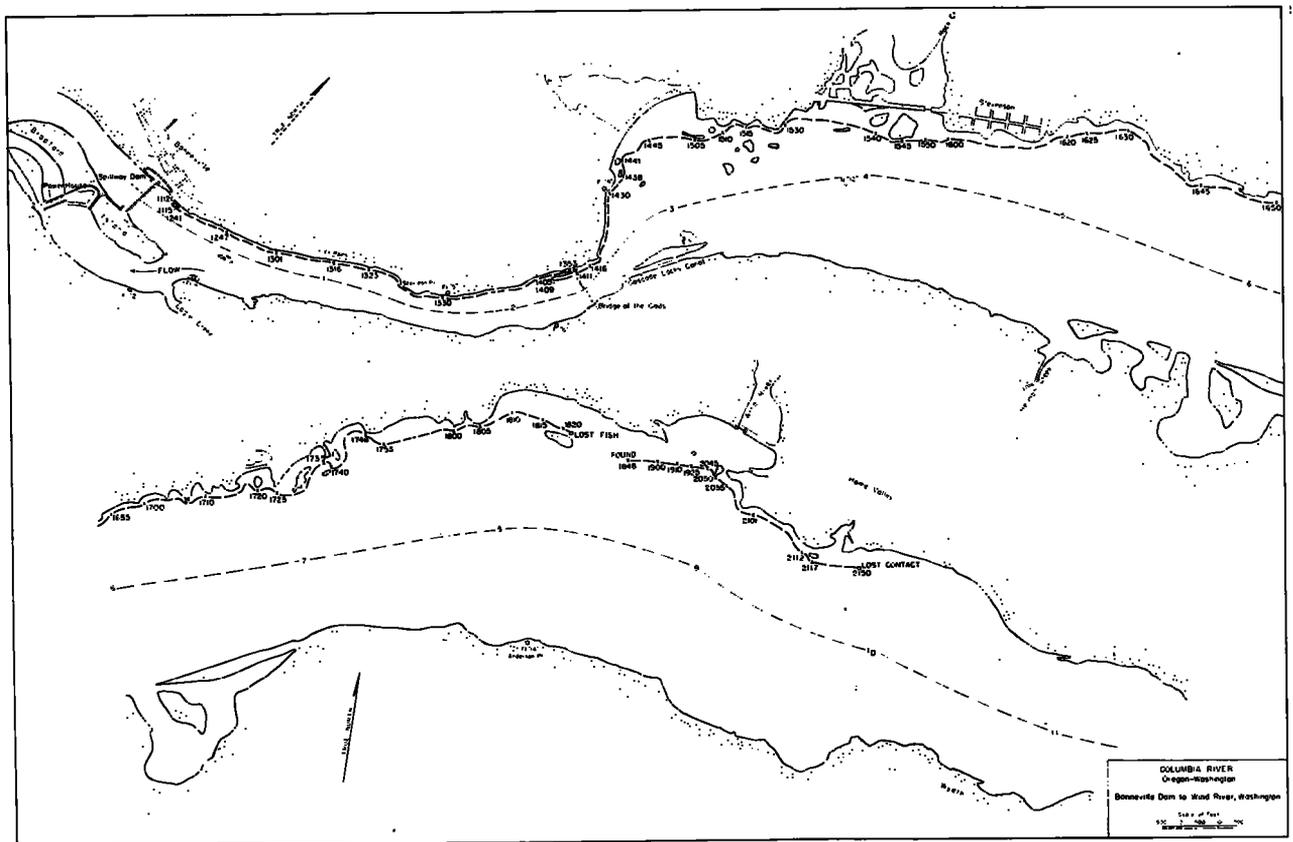


FIGURE 14.—Course of fish tracked September 9, 1957, Columbia River (Washington-Oregon), Bonneville Dam to Wind River, Washington.

Miles upstream from Bonneville Dam spillway indicated by: - - 4 - -

Course of fish and hour of day (military time) indicated by: - - - x - - -
1810

log rafts were tied along shore, in some places extending 400 feet or more into the river. Fish that had previously been swimming upstream at a steady rate usually slowed or stopped completely within a few yards after passing underneath the rafts, then moved slowly and erratically upstream with frequent pauses and occasional back tracks until the rafts were cleared. The fish then resumed the faster steady rate observed before the rafts were encountered. This was the only point above the release area where back tracking was common. Underneath the rafts fish were likely to travel downstream several hundred feet with prolonged pauses at the turning points, but elsewhere the back tracks were rarely as much as 100 feet and the return upstream was more likely to be immediate. One exception was the fish tracked September 9 which moved back 700 feet at the Bridge of the Gods. It was not un-

usual for fish to slow their pace or pause momentarily before passing under the bridge, where the supporting concrete piers created considerable turbulence.

DISCUSSION

The migration pattern of fish in the release area and the pattern of their journey upstream was studied. Because the effects on fish as a result of handling and tagging are difficult to determine, and because some if not all of any resulting impairment presumably diminishes with time, we believe that the movements of fish once they are well underway upstream are probably more nearly representative of their natural behavior than movements during the period prior to their moving out. Comparatively, their movements within the release area were more diverse than were their movements farther upstream, although this behavior might also be true of untagged fish.

TABLE 1.—Release record of sonic-tagged fish tracked at Bonneville Dam, 1957

Date (1957)	Species	Fish length inches	Time held in live box		Time spent in release area		Total number hours tracked	
			Hours	Minutes ¹	Hours	Minutes	Hours	Minutes
Aug. 8	Steelhead	27	17	0	5	3	3	3
14	Chinook	36	1	0	1	1	1	1
14	do	38	1	30	1	1	1	1
15	do	36	2	30	1	1	1	1
15	do	34	1	30	1	1	1	1
16	do	32	1	30	55	55	55	55
19	do	30	1	0	1	1	1	1
20	Steelhead	28	1	0	1	1	1	1
20	Chinook	33	1	30	9	9	9	9
21	Steelhead	28	2	0	12	12	12	12
22	Chinook	20	2	0	40	1	39	39
23	do	34	1	30	10	10	10	10
23	do	36	1	45	2	14	2	31
26	do	36	1	30	1	1	1	1
27	do	34	2	0	22	1	22	22
28	do	32	2	0	22	1	22	22
29	do	34	1	45	28	1	10	10
29	do	42	1	45	59	2	0	0
30	do	36	1	0	54	54	54	54
30	do	38	1	0	9	9	9	9
Sept. 3	do	25	1	30	1	8	45	45
4	do	30	1	30	1	3	49	49
6	do	32	1	45	3	3	3	3
7	do	34	1	45	49	6	42	42
8	do	34	1	0	13	5	4	4
9	do	30	1	5	1	5	5	5
9	do	36	1	30	1	10	38	38
10	do	32	1	30	20	49	49	49
11	do	32	1	30	54	3	44	44
13	do	28	1	30	2	16	43	43
18	do	28	1	15	4	50	7	33
19	do	36	1	0	4	16	7	21
Oct. 2	do	24	1	30	1	53	3	17
4	do	28	1	15	1	1	1	1
4	do	35	1	45	29	29	29	29
5	do	24	1	30	48	48	48	48
6	do	28	1	30	48	9	38	38
7	Steelhead	31	1	15	4	2	58	58
11	Chinook	29	1	15	7	?	3	46
12	Silver	22	1	15	4	53	4	53
13	Chinook	33	1	15	1	33	3	32
14	do	25	1	30	32	1	55	55
15	Silver	24	1	15	12	12	1	41

¹ To nearest quarter hour.² Contact lost before fish left release area.

Since observations were limited to a period when there was little current through the release area, the question arises how nearly did the movements observed correspond to fish movements during periods of greater flow. Of the tracked fish, 70% went below the release point; 9 of them came to within 50 feet of the spill gates. We can only guess whether the number would have been greater had a strong current been moving in the direction of the spillway, or whether, with a strong current by which to orient themselves, the fish would have moved more directly upstream and spent less time wandering in the release area.

To determine whether fish being tracked were influenced by motor noises, propeller turbulence, or possibly the sight of the boat, we attempted on several occasions to herd fish that were moving upstream by approaching them from different

directions. We were unable to cause a fish to change its course or rate of travel.

Effect of tagging and handling

The degree to which fish were affected by handling and tagging is a matter of conjecture. But we do not believe that the sonic tag, used in a quiet stretch of river such as the Bonneville forebay in September and October, seriously affects the natural behavior of adult salmon. The weight of the tag is probably a negligible factor; 2 grams is the maximum weight in water and most tags are within a fraction of a gram of being weightless. However, the tag does create some drag as it moves through the water. We assumed that large fish are less affected by this than small fish. Therefore, at Bonneville, when a choice of size was possible, we selected fish that weighed an estimated 10 pounds or more. The average estimated weight of all fish tagged was 14 pounds and we did not tag a fish weighing less than 5 pounds.

The hog-ring fastener is a probable source of irritation, but while a more refined device is being sought, the present one allows us to tag quickly without removing the fish from the water or immobilizing it. Of the fish tagged at Bonneville, about one in four reacted to tagging by thrashing about in the live box for several seconds before settling down. Others showed no visible reaction.

Possible effects on the fish from sonic properties of the tag are under investigation. So far, we have seen no response by young or adult salmonids to sounds at or near the tag's carrier frequency level of 132,000 cycles per second, even at sound intensities several thousand times greater than that of the tag. It is more likely that they perceive vibrations set up at the tag's pulsing frequency of 1,000 to 2,000 pulses per second. Burner and Moore (1953), working with trout up to 24 inches in length, subjected them to frequencies ranging from 67 cps. to 70,000 cps. and observed that they "started" momentarily as low frequency sounds were turned on, but showed no response to continued sound. (They observed no response by the fish, initial or otherwise, to ultrasonic frequencies.) This momentary reaction pattern was also observed by Moore and Newman (1956) working with salmon fingerlings within a frequency range of 5 cps. to 20,000 cps. They

TABLE 2.—Time, distance, and rate of movement of fish tracked beyond release area

Date	Species	Hour released	Total time fish tracked		Time tracked after fish left release area		Net distance tracked upstream	Average speed after fish left release area	Remarks
		Military time	Hours	Minutes	Hours	Minutes		Miles per hour	
Aug. 8	Steelhead.....	1114	3	03	2	58	3 miles.....	1.0	
20	Chinook.....	1243		56		47	200 yards.....	.1	
22	do.....	0856	1	39		59	150 yards.....	.1	
23	do.....	1121	2	31		17	250 yards.....	.5	
29	do.....	0900	1	10		42	¾ mile.....	1.1	
29	do.....	1258	2	00	1	01	1 mile.....	1.0	
Sept. 3	do.....	0845	8	45	7	37	10 miles.....	1.3	See figs. 5 and 10.
4	do.....	0851	3	49	3	49	6 miles.....	1.6	See fig. 11.
7	do.....	0858	6	42	5	53	7 miles.....	1.2	See fig. 13.
8	do.....	0831	5	04	3	51	4½ miles.....	1.2	See fig. 6.
9	do.....	1112	10	38	9	08	9¾ miles.....	1.1	See fig. 14. Fish traveled 8¾ miles in 6¾ hours before dark.
10	do.....	1244		49		29	¾ mile.....	1.6	
11	do.....	0851	3	44	2	50	3¼ miles.....	1.2	
13	do.....	1102	16	43	13	46	5 miles.....	.4	See figs. 8 and 12. Fish traveled 4½ miles in 5¼ hours before dark.
18	do.....	1122	7	33	2	43	250 yards.....	.1	See fig. 7. Fish entered Eagle Creek 1620 hours and was there 2½ hours later when tracking was abandoned at dark.
19	do.....	1004	7	21	3	05	1¾ miles.....	.6	
Oct. 2	do.....	1325	3	17	1	24	¾ mile.....	.5	
6	do.....	1140	9	38	5	50	½ mile.....	.1	Fish traveled ½ mile in 3 hours before dark;
7	Steelhead.....	1236	5	00		58	400 yards.....	.2	Fish made no sustained movement upstream.
11	Chinook.....	1046	3	46			1 mile.....	?	Lost contact with fish for 3 hours; fish left release area sometime during this period.
13	do.....	0919	3	32	1	59	3¾ miles.....	1.9	
14	do.....	1149	1	55	1	23	2 miles.....	1.5	
15	Silver.....	1246	1	41	1	29	1 mile.....	0.7	

concluded, as did Burner and others, that after the initial "start" the fish quickly adjusted to the new sound and accepted it as part of the large volume of noise normally encountered in the environment. We think it likely that this may also be true with any perceptible sound from the sonic tag.

In a tagging study of this sort, when movements of fish can be measured only over a period of hours rather than days, weeks, or months, any effect from handling a fish prior to release is magnified in the results. We therefore took special care to excite the fish as little as possible. In the dipnet transfer from floating trap to live box they were out of the water a maximum of 5 seconds. Tagging was done while the fish were completely under water and unconfined within the limits of the live box. Although it was unnecessary at any time to place our hands on the fish or in the water, rubber gloves were worn as an extra precaution against the effect of human odor on natural behavior. Finally, the sliding-gate arrangement allowed tagged fish to swim freely out of the live box. In spite of these measures some effect was inevitable but extremely difficult to determine in the field. This problem is therefore being in-

vestigated further at the Fisheries-Engineering Research Laboratory¹ and the Seattle Biological Laboratory² fish behavior facilities.

SUMMARY

1. Thirty-nine Columbia River salmon and four steelhead trout were tagged with miniature sonic transmitters at Bonneville Dam in 1957 and were tracked one at a time. Sound waves from the sonic tag were picked up by an automatic homing receiver mounted in a boat. Data were plotted on charts as a continuous record of individual movements of fish in the Columbia River.

2. All fish were released in the dam forebay near the exit of the Washington-shore fish ladder. The time individual fish took to move out of the release area ranged from less than a minute to nearly 5 hours; the average time was 1½ hours.

3. Seventy percent of the fish traveled some distance downstream from the release point. Nine moved to within 50 feet of the spillway.

¹ Redesignated North Benneville (Wash.) Field Station, U.S. Bureau of Commercial Fisheries, January 1959.

² Seattle Biological Laboratory, U.S. Bureau of Commercial Fisheries, Seattle, Wash.

4. In the release area fish spent more than 90 percent of a total of 47 hours swimming within 50 feet of shore. They seldom left the shoreline for more than 2 minutes at a time.

5. Of 23 fish tracked for some distance above the release area, only 3 crossed to the Oregon shore. One crossed 6 miles above the dam, the other two at Bradford Island.

6. Individual fish were tracked as far as 10 miles upstream and for periods as long as 16½ hours.

7. After the fish left the release area, they rarely swam in water more than 30 feet deep. Where the bottom dropped sharply, fish followed the shoreline closely. Through broad shallow areas individual courses varied more.

8. During hours of daylight fish moved over the bottom at an average rate of approximately 1.5 miles per hour against current ranging in velocity from less than ¼ foot per second to 2 feet per second; their net rate of movement upstream was 1.2 miles per hour.

9. Fish stopped and dropped back frequently where they encountered log rafts tied alongshore. Otherwise, they usually maintained a steady rate of movement after leaving the release area.

10. Each of three fish tracked from daylight into darkness either slowed its pace or came to a complete halt as it grew dark.

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UNITED STATES DEPARTMENT OF THE INTERIOR • Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE • Arnie J. Suomela, *Commissioner*

ABUNDANCE AND LIFE HISTORY OF SHAD ST. JOHNS RIVER, FLORIDA

BY CHARLES H. WALBURG



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ABSTRACT

A method of determining the size and spawning escapement of the shad (*Alosa sapidissima*) population of the St. Johns River, Florida, is presented and population parameters are given for each year 1953 to 1958. Scientific management of the shad population in this river to obtain optimum yields is not possible at this time because factors affecting the size of run are unknown. When data on population size have been obtained for an additional number of years, studies can proceed to determine factors affecting abundance.

Examination of 3,129 scale samples revealed that the majority of shad caught in the St. Johns River are 4 years of age. From the absence of spawning marks on the scales and from other evidence it is apparent that the shad die after their initial spawning run. Females produce 277,000 to 659,000 eggs, and a direct relation exists between the number of eggs produced and the age, length, and weight of the fish. The spawning season extends from late February to mid-April, during which time water temperatures range from 60° to 75° F.

ABUNDANCE AND LIFE HISTORY OF SHAD, ST. JOHNS RIVER, FLORIDA

By CHARLES H. WALBURG, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

During the first half of the twentieth century the commercial catch of American shad, *Alosa sapidissima*, along the Atlantic coast of the United States declined from 48 million pounds to 8 million—a reduction of 83 percent. The fishing industry, through the Atlantic States Marine Fisheries Commission, requested the Federal Government to make a study of the fishery. In 1949, the Congress, in Public Law No. 249, authorized the Fish and Wildlife Service, United States Department of the Interior, to make a comprehensive investigation of the Atlantic coast shad fishery. The objectives of this study, which began in 1950, were (1) to discover causes for decline of the fishery, (2) to determine conditions favoring its recovery, and (3) to provide information for scientific management of the fishery to obtain maximum continuing yields.

The American shad is the largest member of the herring family (Clupeidae) in North American waters. Its range on the Atlantic coast is from the St. Johns River in Florida to the St. Lawrence River in Canada. The shad is anadromous, spending most of its life in the sea, but ascending coastal rivers to spawn. The spawning migration begins as early as November in Florida and as late as June in Canada. Time of spawning migration is at least partially governed by water temperature since few shad enter rivers at temperatures below 40° F. (Talbot 1954; Massmann and Pacheco, 1957). Shad spawn in the fresh-water part of rivers generally at water temperatures between 53° and 68° F. The females deposit their eggs in the open water where fertilization takes place. The number of eggs produced per female ranges from 116,000 to 616,000 (Lehman 1953; Davis 1957). After absorbing water, the eggs sink to the river

bottom but are carried by the current. Hatching occurs in 6 to 8 days, depending on water temperature (Leim 1924).

Talbot and Sykes (1958), using 19 years' tagging data, made an extensive study of shad migrations. According to these authors, shad native to streams north of Cape Hatteras, N.C., that survive spawning, migrate to sea and the following year return to spawn again provided they survive natural and fishing mortalities. Those fish native to streams south of Cape Hatteras die after spawning. The young remain in the rivers until fall, at which time they are 3 to 6 inches in length, and then enter the ocean. They remain in the ocean from 3 to 5 years and at sexual maturity most of them return to the streams of their birth to complete the cycle.

Talbot and Sykes further state that shad from all Atlantic coast rivers spend the summer and fall months in the Gulf of Maine. The fish spend the winter in the Middle Atlantic area, probably in deep water, and with the approach of spring they migrate inshore, destined for their native rivers. This same annual migration is made by the juveniles except they do not enter the rivers until sexually mature.

The shad fishery of the St. Johns River in Florida was first investigated during the winter of 1952–53. Each year from that time through 1958 catch and effort data have been obtained from the commercial fishery and estimated catch data have been obtained from the sport fishery. During the 1957–58 run, the fishery was further investigated to determine fishing rate and size of run for each year 1953 through 1958 and to obtain basic life-history information.

The staff of the Bureau of Commercial Fisheries, Biological Laboratory, Beaufort, N.C., helped with the field studies and reviewed this manuscript. Appreciation is also expressed to

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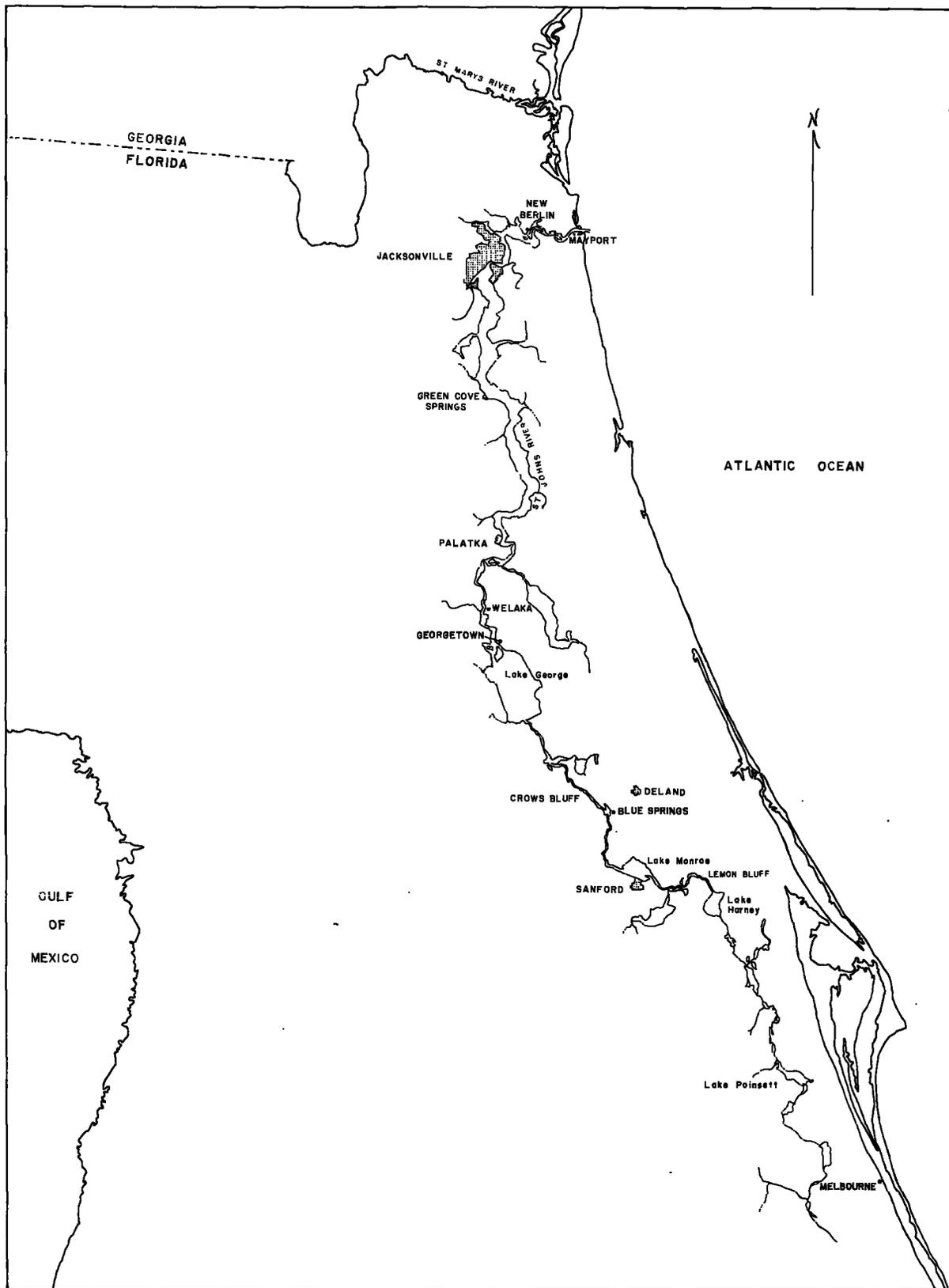


FIGURE 1.—St. Johns River, Florida.

the shad fishermen, fish dealers, and sport-camp operators on the St. Johns River, who cooperated in this study.

THE RIVER AND THE SHAD FISHERIES

The St. Johns River originates in a grassy plain section of Florida about 50 miles north of Lake Okeechobee and 15 miles inland from the State's east coast. It flows north through a chain of lakes for approximately 260 miles to Jacksonville and then turns east and flows 26 miles before emptying into the Atlantic Ocean at Mayport (fig. 1). The St. Johns River differs from other large rivers along the Atlantic coast of the United States in that it flows northward, whereas the other rivers originate farther inland and flow in a southerly direction before entering the ocean.

In its headwaters the St. Johns is not a clearly defined river, since it is shallow, winding, and diffused. In its northward meandering through shallow lakes it creates many diverse channels until Lake Harney is reached. From here to its mouth the river is deeper and has a distinct channel suitable for navigation. Lake George, the only sizable lake existing between the river mouth and Lake Monroe, lies 25 miles south of Palatka and is the approximate head of tidal influence.

In recent years the commercial fishery has operated in widely separated and relatively short stretches of the river. At the mouth, anchor gill nets are fished both north and south of jetties which extend out into the ocean about 1 mile. During the 1958 season, 5,700 linear yards of anchored gill net, 30 to 35 meshes deep and with a stretched-mesh size of 5 to 5¼ inches, were used. In the vicinity of Jacksonville, 26 miles up the river, drift gill nets are used. The three drift gill nets fished in 1958 averaged 100 yards in length and 35 meshes in depth with a stretched-mesh size ranging from 4 to 5¼ inches.

The 55-mile section of the river from Jacksonville to Palatka is broad and composed of numerous flats. No shad fishing is done in this area. Between Palatka and Welaka, a distance of about 20 miles, drift gill nets and haul seines, locally termed shad nets, are used. In 1958 three gill-net operators in the vicinity of Palatka fished 580 linear yards of net. The depth of these nets ranged from 25 to 50 meshes and their stretched-mesh size was 5¼ inches. Nine haul seines totaling 3,240 yards in length were fished between

the Palatka gill-net area and Welaka. These nets ranged in length from 300 to 380 yards, in depth from 20 to 30 feet, and in stretched-mesh size from 2 to 4 inches. No commercial netting was done upstream from Welaka in 1958.

In years previous to 1953, haul seines were fished in the vicinity of Lemon Bluff; since that time, however, commercial shad fishing has been prohibited upstream from the Lake George bar. The legal commercial shad fishing season in the St. Johns River is from November 15 until March 1, but the season can be extended, as occurred in 1958, to March 15 at the discretion of the State Board of Conservation.

Sport fishing for shad is conducted between Lakes Monroe and Harney. There are no legal restrictions on the taking of this species with sport tackle, but there is a creel limit of 15 shad a day.

THE COMMERCIAL FISHERY

According to historical accounts, the first shad fishery in the St. Johns River began in the middle of the nineteenth century. McDonald (1887) quotes R. E. Earll's account of the fishery—

Shad were first caught at Mayport by Charles Waterhouse, of Connecticut, in 1858. He had previously fished in the Savannah, but abandoned it on account of poor results. At Jacksonville gill nets were first used in the shad fisheries in 1868. At Palatka, C. B. Smith, of Connecticut, was the first to establish a shad fishery. He began the work in 1872, and it was not until 1877 that a second fishery was started. In the year 1873, 94,000 shad were caught at New Berlin with thirty nets (an average of 3,133 to the net). From 1865 to 1875 the average catch was 25,000¹ to the net. The year 1876 was the most prolific season of all, when each net averaged a catch of 5,000. In 1875, at Palatka one net caught 11,000 shad, and in the same year it is said six nets took 55,000.

Dr. Charles Kock, in a letter to Mr. Earll from Jacksonville dated January 1874, says—

From the bar at the mouth of the Saint Johns River up to Palatka, seventy-five to eighty nets are fished during the shad season. These nets are about 200 yards long and 10 feet deep (the mesh 1½ inches square), and are set in from 10 to 12 feet of water. In 1874 the product of the shad fisheries amounted to 250,000 shipped or consumed. The average price at Jacksonville, season of 1872-73, was 15 cents apiece.

From available records (table 1) a figure was constructed showing the commercial shad catch made in the St. Johns River for some years, 1880-1958 (fig. 2). These catches (except for

¹ Probably should be 2,500.

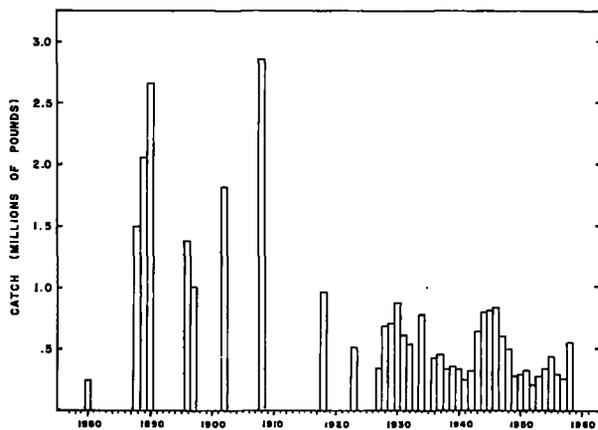


FIGURE 2.—The commercial catch of shad in the St. Johns River for various years, 1880–1958. (See table 1 for source of data. Catch for years 1880–1952 recorded on annual basis and for years 1953–58 on seasonal basis.)

years 1953–58) are recorded for the calendar year rather than for the fishing season. Each fishing season includes the latter part of one year and the early part of the next. Although catch data tabulated on an annual versus a seasonal basis are not strictly comparable, no serious error will result from their comparison here, since less than 20 percent of the seasonal catch is made during the months of November and December. According to data shown in table 1 and figure 2, the fishery reached a peak production of 2,833,000 pounds in 1908. After this time the catch declined drastically and since 1918 has fluctuated between 203,000 and 964,000 pounds. Except for the

TABLE 1.—Commercial catch of shad for various years, 1880–1958, St. Johns River, Florida

[In thousands of pounds. Statistics for 1880–1952 from Power (1956) except as noted; statistics for 1953–58 from this study]

Year	Catch	Year	Catch
1880	252	1899	254
1888	1,448	1940	344
1889	2,051	1941	256
1890	2,654	1942	323
1896	1,375	1943	666
1897	1,011	1944	811
1902	1,819	1945	842
1908	2,833	1946	837
1918	964	1947	625
1923	503	1948	515
1927	348	1949	284
1928	691	1950	298
1929	701	1951	336
1930	880	1952	203
1931	621	1953	280
1932	546	1954	343
1934	782	1955	434
1936	282	1956	293
1937	288	1957	261
1938	229	1958	552

¹ The 1896 catch in fish (Stevenson 1899) converted to pounds by factor of 3.0.

² Data gathered by Florida State Board of Conservation.

period 1953–58, no data are available concerning the amount of gear employed in landing these catches; therefore, it is impossible to say whether fluctuations in catch are attributable to varying fishing intensity, actual changes in shad abundance, or a combination of these factors.

Population Studies, 1953

The shad fishery in the St. Johns River was first investigated by the Fish and Wildlife Service during the 1952–53 season. To avoid confusion, the 1952–53 shad season will be termed the 1953 season, and the 1953–54 shad season the 1954 season, and so on. The purpose of the 1953 study was to determine the total catch, total effort, population size, and spawning escapement. These base-year estimates were to be used with catch and effort statistics collected in subsequent years to determine population parameters for each year in which such data were obtained.

In 1953, catch and effort data were obtained from fish dealers who supplied a daily record of the catch by each fisherman. Tagging studies were conducted from the drift gill-net fishery at Jacksonville and from the haul-seine fishery in the Welaka-Palatka area. An attempt was made to tag from the anchor gill-net fishery at the mouth of the river, but this was unsuccessful because live fish suitable for release could not be obtained. At Jacksonville we were unable to obtain a sufficient number of fish to tag, and in the Welaka-Palatka region an unknown portion of the run had passed through the area before tagging was begun. In addition, some of the fish tagged in the latter area were in poor condition because of higher than normal water temperatures during the winter of 1952–53. Results of the tagging studies at both Jacksonville and in the Welaka-Palatka area were inconclusive and therefore not used for population estimation. Much information concerning the fishery was obtained, however, that was of value to the 1958 investigation.

Catch and Effort Statistics, 1953–58

Catch data have been obtained from the commercial fishery each year since our initial investigation. They were obtained from fish dealers in Mayport, Jacksonville, Palatka, Welaka, and Georgetown, Fla., who purchase all commercially caught shad taken in the St. Johns River (table 2). Effort data in net-days by months were obtained from the haul-seine fishery (table 3). A

TABLE 2.—Commercial catch of shad, by fishing gear and area, St. Johns River, Florida, 1953-58

[In thousands of pounds]

Year	Gill net		Haul seine	Total catch
	Mayport-Jacksonville	Palatka	Welaka-Palatka	
1953.....	60	19	201	280
1954.....	47	35	261	343
1955.....	36	17	381	434
1956.....	99	20	174	293
1957.....	71	8	182	261
1958.....	186	22	344	552

net-day is defined as a day during which a haul seine is used. Total effort is given as the number of net-days for all haul seines. Accurate catch and effort statistics are available from this fishery, since haul-seine operators keep a daily record of the catch made by each net. Comparable effort statistics for the gill-net fishery are not available.

TABLE 3.—Net-days of fishing effort in the haul-seine shad fishery, St. Johns River, Florida, 1953-58

Year	Nov.	Dec.	Jan.	Feb.	Mar.	Total
1953.....		37	466	246	36	785
1954.....	11	47	234	278	46	616
1955.....	11	87	169	146	79	492
1956.....	6	60	108	99	30	303
1957.....	17	47	83	77		224
1958.....	24	64	140	123	75	426

Tagging Study, 1958

The catch and effort data given in tables 2 and 3 can be converted to estimates of population size for each year since 1953 provided an estimate of population size is available for 1 year (Ricker 1940). To obtain this parameter, a tagging and recovery program was conducted during the 1958 season.

Fish for tagging were obtained from the first haul seine encountered by the shad as they moved upstream to the spawning grounds. Tagging was done throughout the fishing season from November 26, 1957, to March 6, 1958. During this period, 950 shad were tagged with Petersen disk tags inserted directly below the origin of the dorsal fin. Care was taken that only vigorous fish were tagged to minimize mortality from the tagging operation. As an incentive for return of tags, a 50-cent reward was paid for each tag returned. Fishermen were contacted frequently to ensure as far as possible that all recaptured tags were recovered.

Ninety-seven tagged fish were recaptured by gill nets. The majority of these (88) were in the Palatka area; 7 were taken at Jacksonville and 2 at Mayport. Since the purpose of the tagging program was to determine the number of shad available to the haul-seine fishery, these 97 tags were subtracted from the total number tagged (950), leaving 853 available to this fishing gear. No tags were recaptured outside of the river; therefore, it is reasonable to assume that most, if not all, tagged fish that moved downstream after tagging eventually resumed their upstream migration to the spawning ground. This same pattern of movement has been assumed in other shad-tagging studies (Walburg 1955) and also in similar work with sockeye salmon, *Oncorhynchus nerka* (Thompson 1945).

During the fishing season, 108 tagged fish were included in the 344,000 pounds of shad which were taken by the haul seines. The estimated fishing rate of these nets was 108/853, or approximately 12.7 percent. Because of the small mesh size of the haul seines all shad encircled by this gear were considered captured regardless of whether they were tagged or untagged.

An estimate of the number of shad available to the haul-seine fishery was made using the following formula:

$$N = \frac{nt}{s}$$

where N = size of population available to haul seines, n = catch by haul seines (344,000 pounds), t = number of tagged fish available to capture (853), and s = number of tagged fish recaptured (108). The estimated number of shad available to haul seines was 2,717,000 pounds. In this study the ratio of the number of fish tagged to the number in the population was relatively low, and therefore confidence limits on the population estimate closely approximate a Poisson distribution. Using Chapman's (1948) equations 43 and 44, 95-percent confidence limits on the population estimates were 2,223,000 and 3,260,000 pounds.

Population Estimates, 1953-58

Before using the catch and effort data for the years 1953 to 1958 to estimate population size, several assumptions must be satisfied (Ricker 1940). They are as follows:

1. Fishing effort is uniform throughout the season.

2. Efficiency, or fishing power, of the fishing gear remains constant within and between years.

3. Migration pattern of the shad is similar each year.

Assumption 1 is not completely satisfied for this fishery. Most fishing is done during January and February (table 3) because market conditions for shad are best during these months. Although fishing effort is not strictly constant over the period of annual exploitation, a similar pattern of fishing is followed each year, and any error introduced by nonuniform effort would therefore be negligible. Assumption 2 is satisfied since the haul seines have been fished by essentially the same crews, in the same manner, and in the same locations each year. Assumption 3 is satisfied since there is no reason to believe that the year-to-year migration pattern of the shad through the haul-seine fishing area is dissimilar even though variable river conditions may alter slightly the initial time of run or affect the speed of upriver migration. These latter effects should balance out over a period of years.

If these assumptions are considered satisfied, the size of the population available to the haul seines can be determined for each year that catch and effort data are available, using a method given by Talbot (1954). The formula is—

$$N = \frac{C}{1 - q^n}$$

where N = number of shad available to haul seines; C = catch by haul seines; n = number of net-days fished by haul seines; and $q = 1 - p$, where p = the fishing power of a haul seine fished for one day, or the ability of a haul seine to catch a certain fraction of the fish present in 1 day's fishing. Using the 1958 data, the value of q was determined from the relation $q^n = \frac{E}{N}$ (Fredin 1954), where E = number of fish escaping the haul seine fishery. Total effort, fishing rate, catch, and estimated size of run available to the haul seines, 1953 through 1958, are given in table 4 as calculated.

To determine the total size of the shad run in the St. Johns River for the years 1953-58, the number of shad taken by gill nets was added to the number available to the haul seines. The commercial fishing rate for these years was determined by dividing the total commercial catch by the

TABLE 4.—*Calculated size of shad run available to haul-seine fishery, St. Johns River, Florida, 1953-58*

Year	Fishing effort (net-days)	Fishing rate (percent)	Catch (in thousands of pounds)	Estimated size of run (in thousands of pounds)
1953.....	785	22.1	201	910
1954.....	616	18.0	261	1,450
1955.....	492	14.5	381	2,628
1956.....	303	9.2	174	1,891
1957.....	224	6.9	182	2,638
1958.....	426	12.7	344	2,709

estimated total population in a given year. Escapement from the commercial fishery was determined by subtracting total catch from population size. Estimates of population size, commercial fishing rate, and commercial fishery escapement for years 1953-58 are shown in table 5.

TABLE 5.—*Population statistics of shad runs, St. Johns River, Florida, 1953-58*

[In thousands of pounds]

Year	Gill-net catch	Size of run available to haul seines	Total population	Total commercial catch	Commercial fishing rate (percent)	Commercial fishery escapement
1953....	79	910	989	280	28.3	709
1954....	82	1,450	1,532	343	22.4	1,189
1955....	53	2,628	2,681	434	16.2	2,247
1956....	119	1,891	2,010	293	14.6	1,717
1957....	79	2,638	2,717	261	9.6	2,456
1958....	208	2,709	2,917	552	18.9	2,365

THE SPORT FISHERY

Sport fishing for shad by hook-and-line has become popular on the St. Johns River in recent years. The first shad was reported taken in this manner in 1942 in the Blue Springs area west of De Land (Snyder 1949). In recent years this fishery has shifted south, and now is pursued between the outlet or western end of Lake Monroe and the inlet or southern end of Lake Harney, a distance of 25 miles (fig. 1). Access to the sport-fishing area at present is limited to nine major landings. Seven of these are privately owned camps and two are public access areas. Sport fishing for shad on the St. Johns is done almost exclusively by trolling from boats with various types of small metal spoons and weighted jigs. The first shad are taken early in December and the fishery usually lasts into April. The best catches are made from the middle of January until the middle of March.

During the 1953 investigation, a limited survey was made to obtain an estimate of the sport catch. Analysis of these data revealed that the catch was

large, approaching one-third the size of the commercial catch. Since the sport catch was of such magnitude, information was obtained each year through 1957 from a major sport-fishing camp, on the number of shad boats rented and the number of shad caught. During the 1958 season, biologists conducted a creel census on the entire sport fishery to determine fishing effort and catch. These data were used together with that collected since 1953 to obtain an estimate of the sport catch for the years 1953-57.

Creel Census, 1958

A voluntary-reporting card system was used in the 1958 creel census. Before the start of the sport-fishing season the census program was explained to all sport-camp operators, and boxes to collect cards were erected at each of the nine major points where shad were landed. The boxes were mounted on posts with signs requesting fishermen to fill out a census card and drop it into the box. Each box had attached to it a supply of cards and a pencil. The census cards were numbered by location and contained space for fishermen to record date, number of persons in party, and number of male and female shad caught.

Biologists visited each landing as often as possible to ensure that a census card was filled out by each fishing party and deposited in the collection box. Effective coverage was possible because of the limited number of fishing areas. In the absence of a biologist, camp operators and boat handlers at each fish camp reminded fishermen to fill out a card. Biologists contacted the maximum number of fishermen during the time of heaviest fishing. In the morning each fish camp was visited and the survey was explained to fishing parties. Also, completed cards from the previous day's fishing were removed from the card box. In the afternoon the areas having large concentrations of fishermen were completely canvassed. Several of the camps are in close proximity and therefore could be checked by one man.

During the first 2 weeks of the survey, the creel census was conducted 7 days a week to acquaint as many fishermen as possible with the program. During the remainder of the study, the census was conducted 5 days a week including all weekends and holidays. Peak fishing activity occurred on weekends and holidays and low activity on Mondays and Tuesdays.

Publicity was given the creel census through newspaper, radio, and television facilities. Life-history and weekly-catch data were furnished these media, and they in turn publicized this information and requested sportsmen to cooperate in the survey.

The sport-fishing season extended over a period of 23 weeks, from November 25, 1957, through May 5, 1958, and during this period an estimated 65,246 shad were caught and kept. This figure was obtained by totaling the catch reported on census cards from all areas. It is probable that a few fishermen made no report of their catches; therefore, the sport-catch estimate is considered minimal. During the creel census, biologists personally checked the catch of fishermen in 2,436 boats who landed 21,462 shad, or 33 percent of the season's catch. The catch included a small number of hickory shad (*Alosa mediocris*) which are identified as American shad by most fishermen and camp operators. The number of hickory shad caught each week was estimated from examination of the catch. Because these two species are not usually differentiated and the proportion of hickory shad in the catch was small (1,553 fish or 2.4 percent), we grouped them together in this study. The weekly catch of both species by sex is shown in table 6. Results of the census show that 13,025 fishermen fishing from 6,002 boats caught an average of 5 shad per fisherman-day, or 10.9 shad per boat-day. The

TABLE 6.—Weekly sport-fishing catch of shad, by species and sex, based on return of census cards, St. Johns River, 1958

Period	American shad			Hickory shad			Total both species
	Male	Female	Total	Male	Female	Total	
Nov. 25-Dec. 1.....	4	3	7				7
Dec. 2-Dec. 8.....	179	133	312				312
Dec. 9-Dec. 15.....	176	101	277	112	11	26	303
Dec. 16-Dec. 22.....	1,258	716	1,974	15	27	139	2,113
Dec. 23-Dec. 29.....	3,644	1,724	4,368	121	112	233	4,601
Dec. 30-Jan. 5.....	2,242	1,536	3,778	75	30	105	3,883
Jan. 6-Jan. 12.....	835	534	1,369	34	18	52	1,421
Jan. 13-Jan. 19.....	1,902	1,547	3,449	54	93	147	3,596
Jan. 20-Jan. 26.....	2,095	1,956	4,051	29	87	116	4,167
Jan. 27-Feb. 2.....	1,765	1,555	3,320	65	98	163	3,483
Feb. 3-Feb. 9.....	2,140	1,896	4,036	18	85	103	4,139
Feb. 10-Feb. 16.....	1,478	1,493	2,971	19	43	62	3,033
Feb. 17-Feb. 23.....	2,058	1,967	4,045	58	85	143	4,188
Feb. 24-Mar. 2.....	3,812	6,348	10,160	38	142	180	10,340
Mar. 3-Mar. 9.....	2,261	3,257	5,518	40	37	77	5,595
Mar. 10-Mar. 16.....	1,617	2,285	3,902	2	5	7	3,909
Mar. 17-Mar. 23.....	637	1,100	1,737				1,737
Mar. 24-Mar. 30.....	757	1,456	2,213				2,213
Mar. 31-Apr. 6.....	1,025	1,964	2,989				2,989
Apr. 7-Apr. 13.....	717	1,059	1,776				1,776
Apr. 14-Apr. 20.....	391	441	732				732
Apr. 21-Apr. 27.....	255	348	603				603
Apr. 28-May 4.....	36	70	106				106
Total.....	30,184	33,509	63,693	680	873	1,553	65,246

peak of the season was reached during the period February 24 through March 2, when 1,285 fishermen boated 10,340 shad.

Estimated Sport Catch, 1953-57

Estimates of the sport-fishery catch for the years 1953-57 are based on data collected in each of these years and on results of the 1958 study. The 1953-57 data were from one of the major sport camps and included the number of shad boats rented and the number of shad caught each day. From the 1958 survey we found that 27 percent of all the boats fished were rented from this camp. Assuming that the same percentage of all the boats fished was rented from this camp each year, an estimate of the number of boats fished each season (1953-57) was calculated (table 7).

To obtain an estimate of the sport-fishery catch each year, 1953-57, the average catch per boat, as determined from the selected sport camp, was multiplied by the estimated number of boats fished each year (table 7). It has been assumed that fishing success (average catch per boat) each year at the selected fish camp was similar to that of the entire sport fishery. This assumption appears justified, since the 1958 study revealed that the average boat caught 10.9 shad a day while those fished from the selected fish camp caught 11.0.

TABLE 7.—*Sport fishery for shad, St. Johns River, 1953-58*
[See text for determination of values]

Year	Sample data			Estimated total		
	Number of boats	Number of fish taken	Average catch per boat	Number of boats	Number of fish taken	Pounds of fish taken
1953.....	961	8,360	8.7	3,600	31,000	82,000
1954.....	726	7,559	10.4	2,700	28,000	74,000
1955.....	912	9,000	9.9	3,400	34,000	90,000
1956.....	699	6,522	9.3	2,600	24,000	64,000
1957.....	1,320	14,269	10.8	4,900	53,000	140,000
1958.....			10.9	6,000	65,000	175,000

The average weight by sex of the shad taken in the sport fishery in 1958 was determined from measurements of 230 males and 198 females. Males averaged 2.1 pounds, and females averaged 3.2 pounds. The sport fishery in 1958 took 30,864 male shad and 34,382 female shad (table 6). Converting this catch to a weight basis, 175,000 pounds were taken in 1958. The ratio of males to females in the catch was not known for years previous to 1958, and therefore it was assumed to be approximately equal. To convert the 1953-57 sport

catch from numbers to pounds, the catches for these years were multiplied by a factor of 2.65, which was the mean weight of a sample of shad composed of equal numbers of each sex in 1958 (table 7).

SPAWNING ESCAPEMENT AND ANNUAL FISHING MORTALITY RATE, 1953-58

Shad which are not taken by the sport fishery are free to spawn and therefore comprise the spawning escapement. To determine the size of the spawning escapement for each year, 1953-58, the total commercial and sport catch was subtracted from the size of run in the same year. The annual fishing-mortality rate was determined by dividing total catch (commercial catch plus sport-fishing take) by size of the run (table 8).

TABLE 8.—*Annual fishing-mortality rate, shad fisheries, St. Johns River, Florida, 1953-58*

[In thousands of pounds]

Year	Size of run	Total catch ¹	Spawning escapement	Annual fishing-mortality rate (percent)
1953.....	989	362	627	37
1954.....	1,532	417	1,115	27
1955.....	2,081	524	1,557	20
1956.....	2,010	357	1,653	18
1957.....	2,717	401	2,316	15
1958.....	2,917	727	2,190	25

¹ Combined commercial and sport fisheries.

LIFE HISTORY OF SHAD

TIME OF RUN

As pointed out previously, shad enter the St. Johns River as early as November and the run lasts until March. Good catches are made at the river mouth during December and February, with the peak catch in the month of January. The relation between time of run and water temperature has long been recognized. Stevenson (1899), quoting from McDonald, discusses this relationship. He stated that shad did not enter the St. Johns River until the water cooled below that of the nearby ocean. This migration began about the last of November when the river temperature at Jacksonville dropped to 60° F. He further stated that shad did not enter other Atlantic coast streams until the temperatures in the rivers warmed above that of the adjacent ocean waters.

The mean monthly temperature of the St. Johns River at Mayport during the period

November through March, 1944 through 1954, ranged from 55° to 72° F. In some years the mean temperature does not reach 60° F., as occurred in the winter of 1949-50 when it ranged from 61° to 66° F. (U.S. Coast and Geodetic Survey, 1955). These data show that shad probably enter the St. Johns over a range of temperatures and do not necessarily delay their entry until the river water cools to 60° F. as reported by Stevenson. This agrees generally with Leach (1925), who stated that shad ascend rivers to spawn when the water temperature is from 56° to 66° F. By way of comparison, Talbot (1954) found that the peak of the run entered the Hudson River at temperatures ranging from 45° to 57° F., which are considerably lower than those found in the St. Johns River.

The mean monthly water temperatures in the river and ocean off the mouth of the St. Johns and Hudson Rivers for the years 1947 to 1954 are shown in table 9. These years are the only ones in which comparable data are available for these stations. From the table it can be seen that temperatures in the St. Johns River at Mayport average colder than in the ocean October through December but warmer during the remainder of the year. The early portion of the run enters when the river temperature is colder than that of the ocean; however, the majority of the run enters in January, February, and March, when the river temperature averages warmer than the ocean. Shad enter the Hudson River during the months of April and May when the river temperature is

TABLE 9.—Mean monthly water temperatures in °F., in river and in ocean off mouths of St. Johns and Hudson Rivers, 1947 to 1954

[Asterisks indicate months in which river temperatures are colder than ocean temperatures. Data St. Johns Lightship from Bumpus (1957); Mayport, Fla., New York City, and Sandy Hook, N.J., from U.S. Coast and Geodetic Survey (1955)]

Month	St. Johns River		Hudson River	
	River ¹	Ocean ²	River ³	Ocean ⁴
January.....	59.8	58.6	39.0	37.4
February.....	59.7	58.7	37.2	36.4
March.....	63.1	61.4	* 39.7	40.4
April.....	68.8	67.1	* 47.2	49.3
May.....	75.8	73.9	* 55.7	57.9
June.....	81.2	79.3	* 65.2	68.2
July.....	82.6	80.6	* 72.1	75.3
August.....	82.5	80.8	* 73.4	74.8
September.....	81.3	80.9	70.8	70.0
October.....	* 74.8	75.0	63.1	60.8
November.....	* 66.1	68.1	53.5	49.9
December.....	* 60.0	60.4	44.5	40.6

¹ Mayport, Fla.

² St. Johns Lightship—off river mouth.

³ New York City at the Battery.

⁴ Sandy Hook, N.J.

colder than the ocean (table 9). Thus it appears that shad will enter the St. Johns River at temperatures above 60° F. For this shad population, at least, some factor other than a temperature differential between river and ocean stimulates them to enter the river. This is evident, since during the early part of the run the temperature of the water in the river is colder than that of the ocean and during the remainder of the run warmer than that of the ocean.

AGE AND GROWTH

Collection and Examination of Material

During 1958, scale samples were collected over the entire season from fish captured by all types of fishing gear. These samples were considered representative of all size classes of shad taken by the fishery. Anchor gill nets and drift gill nets have a large mesh and therefore select the larger fish (mostly females). Haul seines are considered nonselective since their mesh size is small. The sport fishery is also nonselective; however, fishermen prefer female shad. The number of scale samples collected by fishing gear and sex of the fish for which ages were determined are shown in table 10.

TABLE 10.—Number of shad aged, by sex and type of gear, St. Johns River, Florida, 1958

Gear and sex	Number
Anchor gill:	
Female.....	483
Male.....	51
Drift gill:	
Female.....	434
Male.....	163
Haul seine:	
Female.....	572
Male.....	581
Hook and line:	
Female.....	476
Male.....	369
Total.....	3,129

Fork length to the nearest tenth of an inch, weight in ounces, and sex were determined for each fish from which scales were obtained. For consistency, all scales were taken from the left side of the fish, at about one-half the body depth and below the origin of the dorsal fin. In this area, shad scales are most symmetrical and therefore more accurately aged and measured for growth determinations.

Shad scales are not tightly imbedded and therefore are easily lost. Lost scales are replaced with scales of a regenerative type that do not show

all the growth rings. In the laboratory, each scale sample was examined before it was mounted and regenerative-type scales were discarded. Plastic impressions were made of two scales from each fish. The method used to age shad scales is described by Cating (1953), in which transverse-groove counts are used as an aid to determine location of annuli. Each fish was aged by two readers working independently and using an Eberbach projector. Scales for which age readings were in disagreement were re-read, and in most cases agreement was reached. Approximately 3 percent of the scales were discarded as unreadable. The validity of annuli as true year-marks on shad scales has been established by LaPointe (1958). In the present study the edge of the scale was termed an annulus since the fish were captured on their spawning run. Studies at the Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C., indicate that the annulus is laid down on the shad scale during the late winter and early spring months. The positions of the focus and of the annuli on each scale were marked on strips of paper. A nomograph (Carlander and Smith, 1944) was then used to determine the fork length of the fish at time of annulus formation.

Body-Scale Relation

The body-scale relation was determined from a sample of 242 adult shad ranging in fork length from 12.8 to 18.8 inches. Fish were selected by 0.1-inch size classes by sex, and when available three fish were chosen as being representative of each size group. The body-scale relation was found to be similar for both sexes, and therefore the data were grouped, sexes combined, into 0.5-inch size classes as shown in table 11. The relation between fork length and scale radius was found to be highly correlated ($r=0.99$). The body-scale relation over the range of the data was linear. The regression equation obtained for fitting a straight line to the means of anterior scale radii and fork lengths was—

$$L=1.550S-0.156$$

where L =fork length in inches and S =anterior scale radius (inches $\times 26.7$). The relation between average fork lengths and average scale radius is shown graphically in figure 3. Leim (1924) working on fish from the Shubenacadie

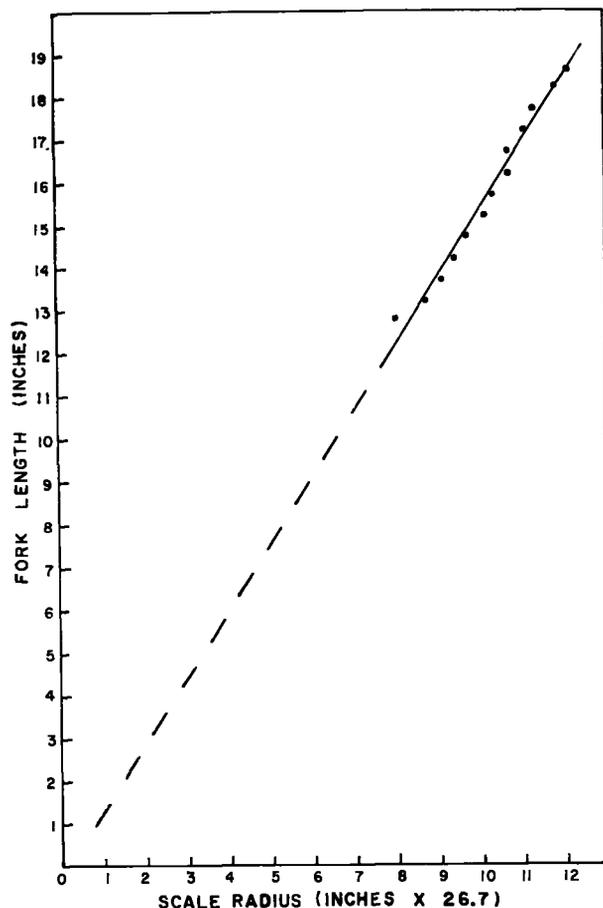


FIGURE 3.—Body-scale relation in shad of the St. Johns River.

River in Nova Scotia has shown that the length of shad at time of scale formation is approximately 27 mm. (1.1 in.). The intercept of the regression line (-0.2 in.) in figure 3 does not cross the axis of fish length at the time of scale formation. From this it is apparent that

TABLE 11.—Relation of scale radius ($\times 26.7$) to fork length in shad, sexes combined, St. Johns River, Florida

[In inches]

Fork length	Number of fish	Average fork length	Average scale radius
12.5-12.9	1	12.8	8.0
13.0-13.4	10	13.2	8.7
13.5-13.9	17	13.7	9.1
14.0-14.4	17	14.2	9.4
14.5-14.9	19	14.7	9.7
15.0-15.4	25	15.2	10.1
15.5-15.9	30	15.7	10.3
16.0-16.4	30	16.2	10.7
16.5-16.9	30	16.7	10.7
17.0-17.4	24	17.2	11.1
17.5-17.9	15	17.7	11.3
18.0-18.4	15	18.2	11.8
18.5-18.9	9	18.6	12.1

these observations on adults cannot be extrapolated to show the body-scale relation in young shad. LaPointe (1958), working with data from both juveniles and adults, used a curvilinear regression line to describe the body-scale relation in shad from three rivers.

Age and Spawning-Class Distribution

The age-class distribution of 3,129 shad sampled from the commercial and sport fisheries is shown in table 12. All shad were on their initial spawning run. The majority of both males and females were 4 years old; however, a larger percentage of females than males were 5 years of age and older. In a similar study on the Hudson River, Talbot (1954) also found that shad spawned for the first time predominately at 4 to 5 years of age; however, as can be seen in table 13, St. Johns River fish mature and spawn at an earlier average age. Unpublished scale data collected in other years on these rivers are in agreement with this finding.

TABLE 12.—Age-class distribution of shad, by sex, St. Johns River, Florida, 1958

Age class	Male		Female	
	Number	Percent	Number	Percent
II.....	1	+		
III.....	129	11	9	+
IV.....	887	76	1,365	70
V.....	140	12	544	28
VI.....	7	1	46	2
VII.....			2	+
Total.....	1,164	100	1,965	100

+ Less than 0.5 percent.

TABLE 13.—Age distribution at first spawning of shad from St. Johns River in 1958 and Hudson River in 1950 and 1951

[Sexes combined. Hudson River data from Talbot (1954)]

Age class	St. Johns (percent)	Hudson (percent)
II.....	+	+
III.....	4	6
IV.....	73	47
V.....	22	36
VI.....	2	10
Over VI.....	+	1

+ Less than 0.5 percent.

Not any of the scales collected from shad of the St. Johns River in 1958 contained spawning marks. These are scarlike rings formed on the scales each year that the shad spawns (Cating 1953). This was also true for 730 samples collected in 1953 and 228 collected in 1950 by B. O. Freeman of the

Florida Game and Fresh Water Fish Commission. These findings indicate that St. Johns River shad die after they spawn. Since shad generally sink after death, a mass mortality may not be obvious; however, persons frequenting the area of the spawning grounds in April and May have reported that weak and dying shad were being consumed by large numbers of white pelicans.

Additional evidence that these fish do not survive spawning was found in the 1953 tagging studies on the river. Approximately 600 tagged shad were not recovered in the fishery that year and therefore would be free to spawn. If they survived they could return to the sea and the following year re-enter the river to spawn. The fishery was canvassed after the 1954 fishing season, but not one of these tags was recovered. The fishery was also investigated after the 1959 season, but no shad tagged in 1958 was recovered, a further indication that these fish do not survive spawning.

Previous studies have shown that shad native to other streams south of Cape Hatteras also die after spawning (Sykes 1956; Walburg 1956, 1957). In contrast, shad that have spawned the previous year make up to 27 percent of the commercial catch in Chesapeake Bay (Walburg and Sykes, 1957) and up to 50 percent of the commercial catch in the Hudson and Connecticut Rivers (Talbot 1954; Moss 1946).

Growth of Shad

The sample of 242 fish used to determine the body-scale relation was also used to study average growth rate of St. Johns River shad (table 14). At any given age, the females were consistently larger than the males, and this difference in average length tended to increase with age.

Since shad enter this river over a prolonged period (November to March), a study was made to determine if any significant difference in the past year's growth increment occurred between fish of the same age entering the river early and those entering late in the run. This comparison revealed only small differences of less than 0.1 inch. From this we can conclude that annual growth was either essentially complete before the first shad entered the river or that those shad which entered late in the run continued their growth in the ocean and at the time of entrance into the river had attained a growth similar to that of the early arrivals.

TABLE 14.—Growth rate of shad, by age class and sex, St. Johns River, Florida, 1958
[Lengths in inches. M=male; F=female]

Age class	Number of fish	Sex	Fork length at capture	Calculated fork length corresponding to annulus number								
				1	2	3	4	5	6	7		
III.....	37	M	13.7	6.8	11.3	13.7	-----	-----	-----	-----	-----	-----
III.....	5	F	14.3	7.0	11.6	14.3	-----	-----	-----	-----	-----	-----
IV.....	60	M	15.3	6.8	11.5	13.7	15.3	-----	-----	-----	-----	-----
IV.....	66	F	16.2	7.0	12.0	14.3	16.2	-----	-----	-----	-----	-----
V.....	26	M	16.7	6.8	11.4	13.6	15.4	16.7	-----	-----	-----	-----
V.....	37	F	17.7	7.1	11.7	14.1	16.2	17.7	-----	-----	-----	-----
VI.....	2	M	17.2	6.4	10.6	12.6	14.4	16.2	17.2	-----	-----	-----
VI.....	7	F	18.2	7.1	11.1	13.2	15.2	16.9	18.2	-----	-----	-----
VII.....	2	F	18.4	6.9	11.0	12.8	14.4	16.0	17.4	18.4	-----	-----
Total and weighted average length.....	125 117	M	-----	6.8	11.4	13.7	15.3	16.7	17.2	-----	-----	-----
		F	-----	7.0	11.8	14.1	16.1	17.5	18.0	18.4	-----	-----
Length increment.....	-----	M	-----	6.8	4.6	2.3	1.6	1.4	0.5	-----	-----	-----
		F	-----	7.0	4.8	2.3	2.0	1.4	0.5	0.4	-----	-----

Length samples obtained from the haul-seine fishery indicate that the early run was generally made up of fish that averaged larger than those making up the remainder of the run (table 15). This was true not only for length but also for weight.

From the 3,129 fish sampled in this study, it was determined that the average fork length of males was 15.6 inches (range 12.0–17.6) and of females 16.8 inches (range 15.1–19.1). The average weight was 2.2 pounds (range 1.0–3.8) for males and 3.1 pounds for females (range 1.8–5.0).

TABLE 15.—Average fork length of shad captured by haul seine, by sex and month, St. Johns River, Florida, 1958

[In inches]

	Male		Female	
	Number	Average fork length	Number	Average fork length
December.....	132	15.7	109	17.2
January.....	194	15.1	195	16.8
February.....	175	15.0	159	16.7
March.....	90	15.2	115	16.8
Mean length (weighted).....	-----	15.2	-----	16.8

FECUNDITY

The ova production of St. Johns River shad was determined from 19 ovary samples obtained during the period February 19 through March 11, 1958. To ensure that only unspawned females were selected, the samples were taken from the haul-seine fishery, approximately 90 miles downstream from the spawning area. The paired ovaries from each shad sampled were removed, wrapped in gauze, and preserved in

10-percent formalin. The fish ranged in fork length from 13.9 to 18.1 inches and in weight from 21 to 65 ounces. Age readings indicated that the fish were from 4 to 6 years of age.

The wet-weight method was used to determine the number of eggs in ovaries as described by Lehman (1953). In the present study, however, sample aliquots were taken only from the center portion of each ovary. The validity of this method of sampling to estimate ova production of shad was demonstrated by Davis (1957).

This study indicated that ova production ranged from 277,000 to 659,000 eggs (table 16). The relation between ova production and weight of the fish is shown in figure 4. A least squares regression line fitted to these data is described by the formula—

$$Y = 8.084X + 65.405,$$

where Y = ova production and X = fish weight in ounces. The relation of these variables is linear ($r=0.90$). A direct relation between increase in egg production and increase in age or fork length is also evident from inspection of table 16.

Lehman (1953) found that ova production of Hudson River shad ranged from 116,000 to 468,000 eggs. The fecundity of St. Johns River shad is therefore greater despite the fact that fish from the Hudson average older and larger than those from Florida.

SPAWNING GROUNDS

A study to locate the spawning grounds in the St. Johns River was made during the 1953 investigation. Twenty-eight sampling stations were established between the south end of Lake George

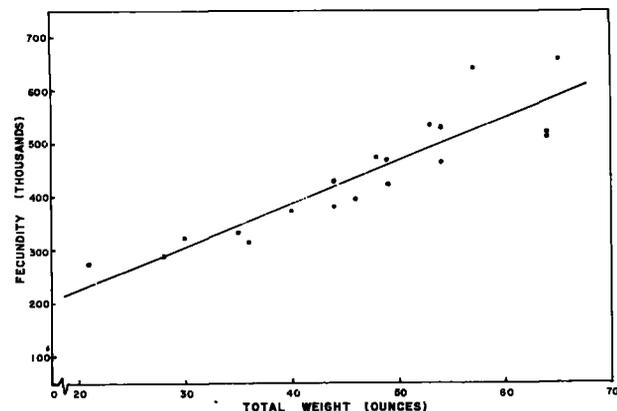


FIGURE 4.—Relation between number of ova produced and total weight of 19 shad, St. Johns River, 1958.

TABLE 16.—*Estimated ova production of 19 female shad, St. Johns River, Florida, 1958*

Date of capture	Fork length (inches)	Total weight (ounces)	Age (years)	Weight of ovaries (grams)	Mean number of ova per gram	Estimated number of ova (thousands)
Mar. 5	13.9	28	4	101.86	2,856	291
11	14.4	30	4	159.70	2,026	324
1	14.5	21	4	96.42	2,868	277
1	14.9	35	4	158.17	2,107	333
5	15.4	36	4	144.30	2,186	315
4	15.4	40	4	216.61	1,727	374
7	15.8	44	4	147.25	2,901	427
Feb. 27	15.9	46	5	148.82	2,662	396
25	16.4	44	4	197.06	1,938	382
27	16.4	48	4	195.52	2,432	476
21	16.8	49	4	213.38	2,204	470
Mar. 1	16.8	54	4	276.74	1,678	464
Feb. 19	16.9	53	5	221.10	2,434	538
Mar. 1	17.0	49	5	176.79	2,396	422
1	17.2	57	5	257.32	2,502	644
Feb. 19	17.5	64	6	274.82	1,894	521
25	17.7	54	5	222.49	2,394	533
25	18.0	64	5	234.72	2,210	519
21	18.1	65	6	288.90	2,281	659

and the source of the river near Melbourne, Fla., a distance of approximately 115 miles. The survey was begun in mid-February when the first spawned-out shad were observed in the Sanford area and continued until the middle of April when spawning was essentially complete. Cone-shaped nets made of fine-meshed nylon, with a diameter of 1 meter and a length of 3 meters, were used to obtain samples of eggs by anchoring them to the river bottom so that the current swept through them. For a more detailed description of this net and how it is fished see Massmann (1952).

Analysis of the data obtained from egg-net sampling revealed that the spawning area extended from Crows Bluff west of De Land to approximately 10 miles south of Lake Harney. The largest number of eggs was found in the area between the south end of Lake Monroe and the highway bridge immediately south of Lake Harney. In both 1953 and 1958 the shad spawning season extended from the latter part of February until the middle of April. The water temperature at the outlet of Lake Monroe during these months ranged from 60° to 75° F.⁴

DISCUSSION

Scientific management of the shad population of the St. Johns River to obtain optimum yields is not now possible because the factors that affect size of the run are unknown. A number of elements could have an effect on the population by either increasing or decreasing its size. Some examples are fishing, pollution, water temperature,

streamflow, predation, and competition. Since the magnitude of the population is known for only 6 years, no conclusions can be made as to causes for fluctuations in abundance. After population parameters have been determined for an additional number of years, hypotheses may be formulated to account for changes in abundance. If factors affecting these changes can be determined and controlled, the shad population can then be managed on an optimum sustained yield basis. However, if the factors cannot be controlled, their effect could probably be predicted and the fishery managed accordingly.

SUMMARY

The shad fishery of the St. Johns River in Florida was studied during the winters of 1953 and 1958 as part of a coastwise investigation of the American shad begun by the Fish and Wildlife Service in 1950. The purpose of the present study was to obtain catch and effort data from the commercial and sport fisheries, fishing mortality rate, size of run, and basic life history information.

Shad fishing on the St. Johns River is conducted in widely separated and relatively short stretches of river. Anchor gill nets are fished at the mouth of the river, drift gill nets are fished in the vicinity of Jacksonville and Palatka, haul seines are fished between Welaka and Palatka, and a sport fishery is operated in the Sanford area.

Commercial shad fishing began in 1858. According to available records, the peak catch was made in 1908 when 2,833,000 pounds were landed. Since 1918, the catch has fluctuated between 203,000 and 964,000 pounds.

Since 1953, effort data have been obtained from the haul-seine fishery, and catch data have been obtained from both the commercial and sport fisheries. From a tagging study and analysis of catch and effort data, it was calculated that 2,709,000 pounds of shad were available to the haul-seine fishery in 1958. In this same year, gill nets caught 208,000 pounds of shad. Adding this catch to the number of pounds of shad available to the haul seines, the estimated size of the 1958 run was 2,917,000 pounds. With the basic population data obtained in 1958 and the catch and effort data collected since 1953, population size was determined for each year 1953 to 1957.

After shad pass through the commercial fishing area, they are subject to capture by the sport

⁴ Water temperatures obtained from Florida Light and Power Company, Sanford, Fla.

fishery which operates between Lake Monroe and Lake Harney. During the 1958 study, a creel census was conducted on this fishery to determine fishing effort and size of catch. Partial data on this fishery were obtained each year since 1953. This information, together with that obtained in 1958, was used to obtain an estimate of the sport catch for each year 1953 to 1957.

Shad that escape the sport fishery are free to spawn and therefore comprise the spawning escapement. This escapement was determined for each year by subtracting both the commercial and sport catch from size of run.

Scale samples and length and weight data were obtained from 3,129 shad taken by all types of gear fished in the river. Age readings revealed that the majority of both males and females were 4 years old; however, a larger percentage of females were 5 years of age and older. Since scale readings indicated that all fish were spawning for the first time and since tagged fish were not recovered the year after tagging, it appears that St. Johns River shad die after their initial spawning run.

At any given age the females were larger than the males, and this difference tends to increase with age. The average fork length of males was 15.6 inches and that of females 16.8 inches. The average weight of males was 2.2 pounds and that of females 3.1 pounds.

Ova production ranged from 277,000 to 659,000 eggs, and there was a direct relation between egg production and age, length, and weight of the fish. Studies revealed that the spawning area extended from Crows Bluff west of De Land to approximately 10 miles south of Lake Harney. The spawning season extended from the latter part of February to the middle of April, during which time the water temperature ranged from 60° to 75° F.

Management of the shad population of the St. Johns River on an optimum sustained yield basis is not now possible because the factors that affect size of run are unknown. When population parameters have been determined for an additional series of years, studies can proceed to determine factors affecting population abundance.

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