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DEVELOPMENT OF EGGS AND LARVAE OF PACIFIC MACKEREL AND DISTRIBUTION AND ABUNDANCE OF LARVAE 1952-56

BY DAVID KRAMER
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FISHERY BULLETIN 174
From Fishery Bulletin of the Fish and Wildlife Service
VOLUME 60

PUBLISHED BY U.S. FISH AND WILDLIFE SERVICE • WASHINGTON • 1960
PRINTED AT U.S. GOVERNMENT PRINTING OFFICE, WASHINGTON

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington 25, D.C. Price 35 cents

Library of Congress catalog card for the series, Fishery Bulletin of the Fish and Wildlife Service:

U.S. *Fish and Wildlife Service.*
Fishery bulletin. v. 1–

Washington, U.S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.

Bulletins composing v. 47– also numbered 1–

Title varies: v. 1–49, Bulletin.

Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239*

Library of Congress [59r55b1]

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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, zygopophyses, 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. Thrailkill 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 *pneumatos*, 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 Fitch [1] 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 (Fitch [2]): 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 (Fitch [2]); 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 Gigedo 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]	0.26	
Fry	do	June–July	[2]	0.9–1.2	1.05–1.08	[2]		
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 amost 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

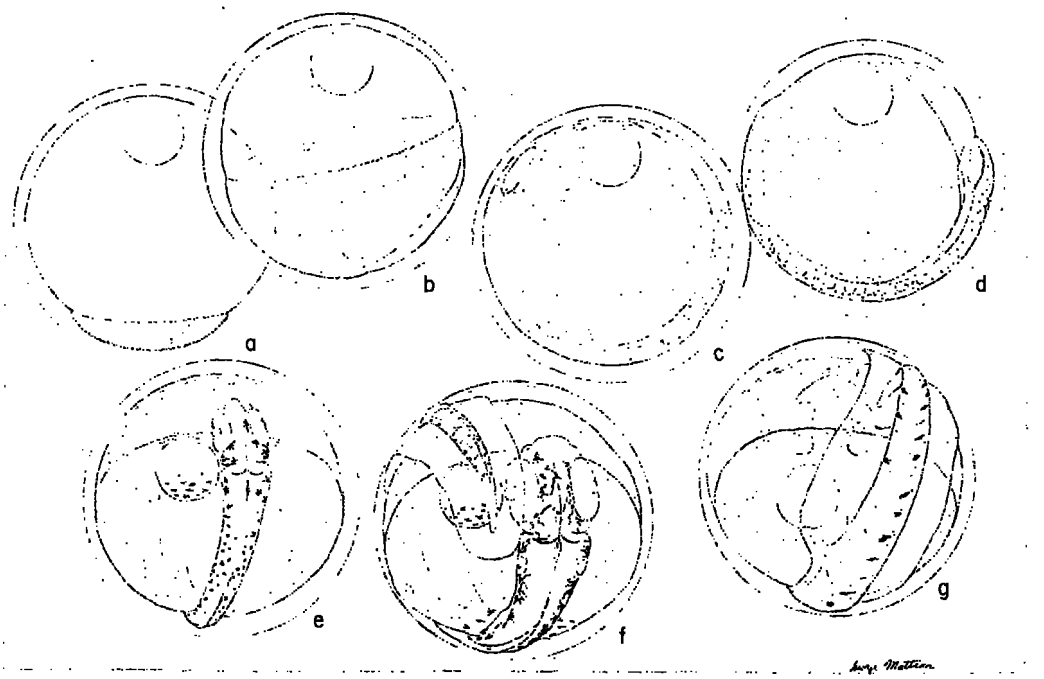

FIGURE 1.—Development of the egg of the Pacific mackerel, *Pneumatophorus diego: a*, *b*, and *c*, early embryonic development, *c* being the early stage immediately before blastopore closure; *d*, middle-stage, just after blastopore closure; *e*, middle-stage, dorsal view of head and pectoral region, 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.

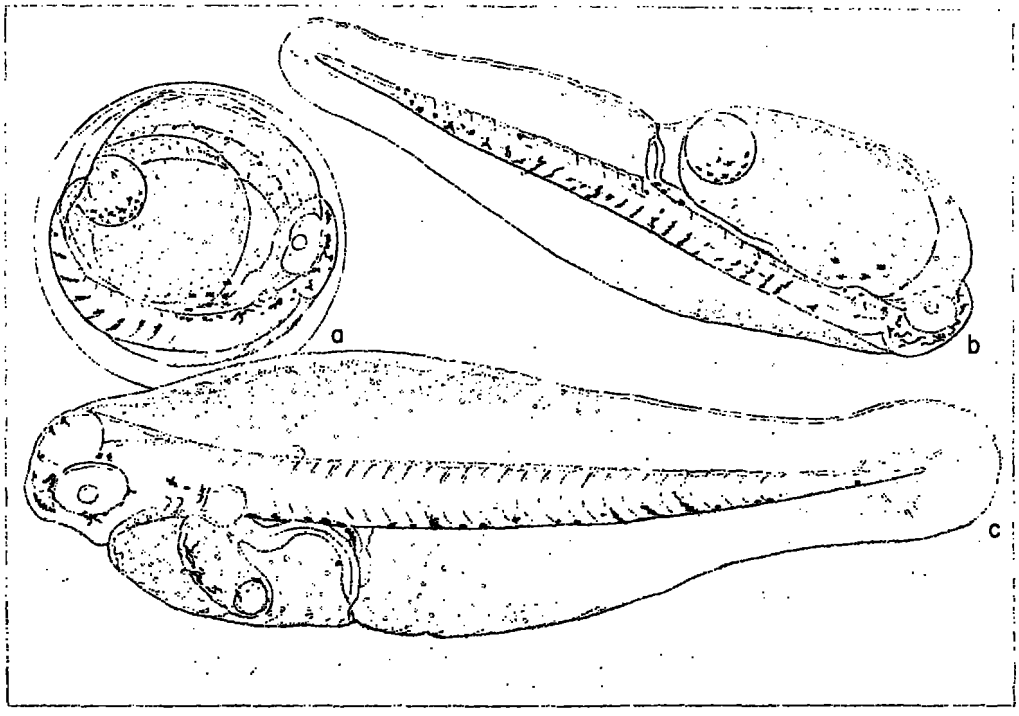

FIGURE 2.—Late-stage egg and yoke-sac larvae of the Pacific mackerel, *Pneumatphorus diego: a*, egg immediately before hatching; *b*, yoke-sac larva, 3.3 mm. long, just after hatching; *c*, yoke-sac larva, 3.5 mm. long, with yoke about two-thirds absorbed.

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 15*e*, but this larva was no more developed than that of a 6.0 mm. larva (fig. 15*a*) 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 (1936a; 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 (1936a; 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

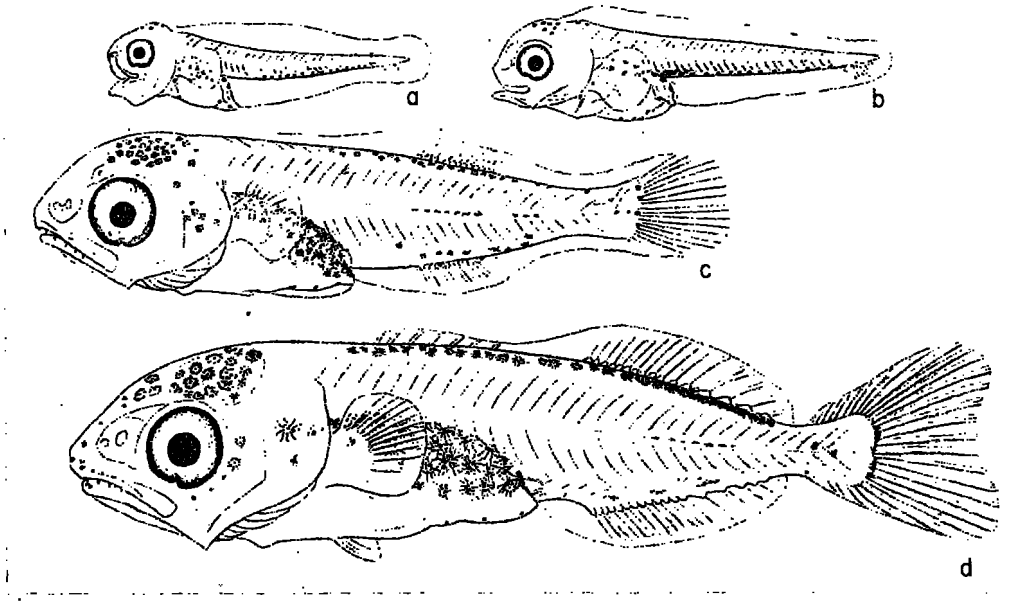

FIGURE 3.—Development of the larva of the Pacific mackerel, *Pneumatophorus diego: a*, larva 4.0 mm. long; *b*, larva 5.0 mm. long; *c*, larva 7 8 mm. long; *d*, larva 10.5 mm. long.

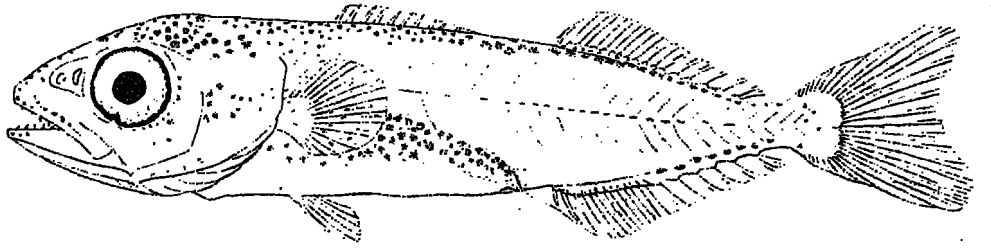

FIGURE 4.—Late larva of the Pacific mackerel, *Pneumatophorus diego*, 16.5 mm. long.

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. 3*c*). 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 meristic[3] 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 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.

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] YS	1.17	-------	-------
2.50–2.99	21	2.78	0.65	0.31	YS	1.19	-------	-------
3.00–3.49	12	3.25	0.76	0.40	YS	1.50	-------	-------
3.50–3.99	2	3.64	0.93	0.43	YS	1.71	-------	-------
4.00–4.49	7	4.25	1.00	0.49	0.99	1.96	-------	-------
4.50–4.99	17	4.72	1.20	0.57	1.17	2.31	-------	-------
5.00–5.49	14	5.30	1.34	0.61	1.31	2.59	-------	-------
5.50–5.99	29	5.74	1.51	0.68	1.46	2.92	-------	-------
6.00–6.49	24	6.24	1.66	0.74	1.62	3.25	-------	-------
6.50–6.99	23	6.70	1.78	0.79	1.71	3.55	-------	-------
7.00–7.49	20	7.23	1.95	0.83	1.88	3.90	-------	-------
7.50–7.99	5	7.76	2.09	0.87	1.95	4.16	-------	-------
8.00–8.49	16	8.21	2.35	0.99	2.20	4.71	-------	-------
8.50–8.99	5	8.79	2.49	1.06	2.31	5.05	-------	-------
9.00–9.49	11	9.33	2.59	1.06	2.40	5.28	-------	-------
9.50–9.99	2	9.72	2.80	1.09	2.50	5.60	-------	-------
10.00–10.49	4	10.22	2.89	1.12	2.58	6.34	-------	-------
10.50–10.99	2	10.68	3.10	1.18	2.74	6.38	-------	-------
11.00–11.99	6	11.37	3.27	1.25	2.85	7.02	4.32	7.36
12.00–12.99	1	12.70	3.75	1.48	3.20	7.90	4.80	8.25
13.00–13.99	5	13.50	3.92	1.42	3.22	8.48	5.10	8.77
14.00–14.99	4	14.49	4.19	1.40	3.36	9.18	5.57	9.56
15.00–15.99	4	15.48	4.45	1.50	3.42	9.80	5.85	10.20
16.00–16.99	5	16.55	4.78	1.58	3.62	10.54	6.28	10.77
17.00–17.99	3	17.20	4.95	1.64	3.82	10.92	6.42	11.14
18.00–18.99	1	18.90	5.50	1.71	4.00	12.60	6.80	12.40

[1] See appendix for data on all specimens.
[2] Yolk-sac stage.

[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 larvae* [1]

[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						[3] LB							
2.50–2.99	21						LB							
3.00–3.49	12						LB							
3.50–3.99	2						[4] LP							
4.00–4.49	7		1 or 2				LP							
4.50–4.99	17		1–4	2–8			LP							
5.00–5.49	14		1–5	8–10			LP							
5.50–5.99	29		3–5	7–16			LP							
6.00–6.49	24		3–6	6–17		1	LP							
6.50–6.99	23	5–14	4–6	10–17		1	5	5						
7.00–7.49	20	4–16	5 or 6	10–17		1	2–5	2–5						
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	1
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		IX	2 and 3
11.00–11.99	6	31	7	17	3–6	3–6	10–14	10–14	11–I, 11	I, 11	5–6½	5–6½	VI–VIII	1–I, 3 or I, 4
12.00–12.99	1	31	7	17	7	7	15	15	I, 11	II, 11	6½	6½	X	I, 5
13.00–13.99	5	31	7	17	6 or 7	6–8	13–15	14 or 15	I, 11	II, 11	6½	6½	X	I, 3–I, 5
14.00–14.99	4	31	7	17	6 or 7	6 or 7	15	14–16	I, 11	II, 11	6½	6½	X	I, 5
15.00–15.99	4	31	7	17	7 or 8	7 or 8	16 or 17	15–18	I, 11	II, 11	6½	6½	X	I, 5
16.00–16.99	5	31	7	17	7–9	7–9	16 or 17	15–18	I, 11	II, 11	5 or 6½	6½	IX or X	I, 5
17.00–17.99	3	31	7	17	9	9	17	17 or 18	I, 11	II, 11	6½	6½	X	I, 5
18.00–18.99	1	31	7	17	9	9	17	18	I, 11	II, 11	6½	6½	X	I, 5

[1] See appendix for data on all specimens.
[2] Second dorsal, anal, and ventral fins; arabic numeral alone represents early development; no differentation 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 differentation 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	26.59	11.81	25.59	53.00		
7.00–7.49	7.23	26.99	11.55	25.95	53.99		
7.50–7.49	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	8.79	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	64.35
12.00–12.99	12.70	29.53	11.65	25.20	62.20	37.80	64.96
13.00–13.99	13.50	29.04	10.51	23.83	62.78	37.54	64.65
14.00–14.99	14.49	28.90	9.68	23.14	63.35	38.44	65.96
15.00–15.99	15.48	28.75	9.70	22.06	63.30	37.79	65.52
16.00–16.99	16.55	28.90	9.54	21.99	63.70	37.96	65.07
17.00–17.99	17.20	28.76	9.52	22.19	63.52	37.35	64.76
18.00–18.99	18.90	29.10	9.05	21.16	66.67	35.98	65.61

[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 ossification of the premaxilliaries all distances were measured from the most anterior point of the premaxilliaries 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	$s_{y.x}$
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	3. 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.
$s_{y.x}$=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.

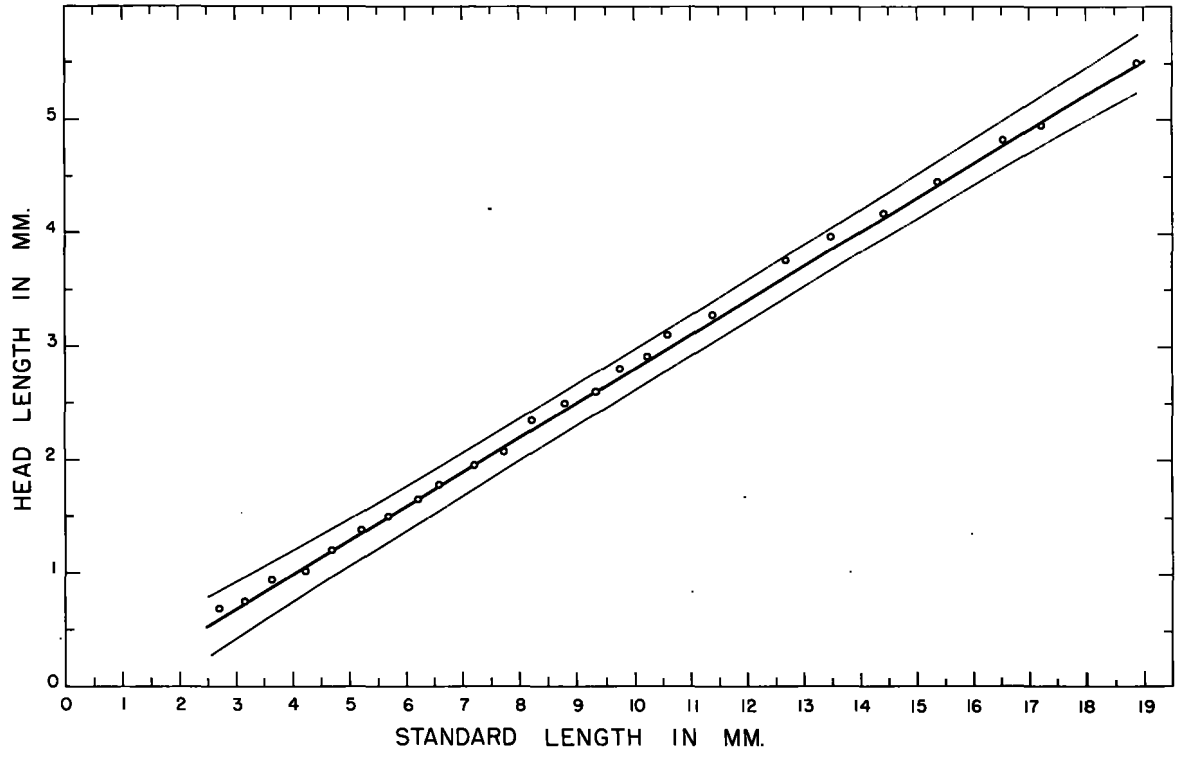

FIGURE 5.—**Regression of head on standard length (middle line). The line is fitted to the data by the method of least squares, using all measured specimens. Each circle is the average of a group of measurements (see table 3, columns 2, 3, and 4). Statistics describing the line are given in table 6. The outer lines are the curves of 95 percent confidence limits.**

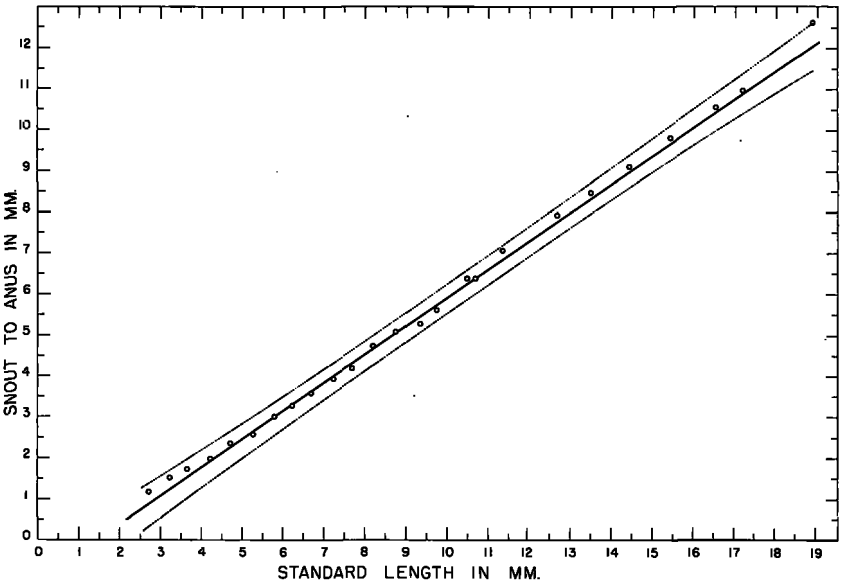

FIGURE 6.—Regression of distance from snout to anus on standard length (middle line). The line is fitted to the data by the method of least squares, using all measured specimens. Each circle is the average of a group of measurements (see table 3, columns 2, 3, and 7). Statistics describing the line are given in table 6. The outer lines are the curves of 95 percent confidence limits.

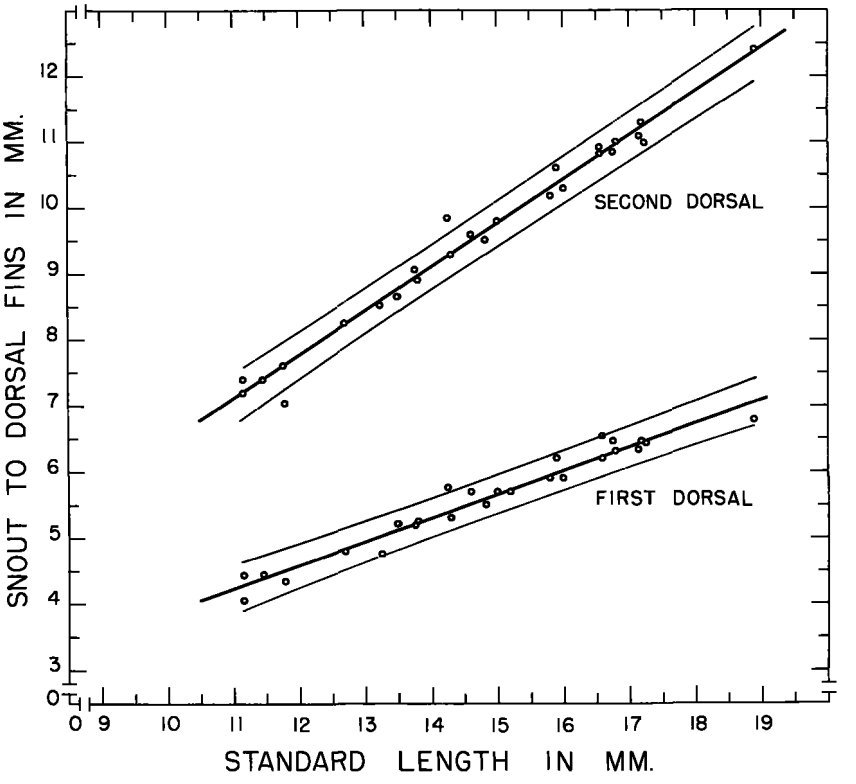

FIGURE 7.—Regressions of the distances from the snout to the first and second dorsal fins on standard length (middle line of each group). The lines are fitted to the data by the method of least squares, using all measured specimens. Each circle is the measurement from the snout to the origin of the fin (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 subopercular.

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.

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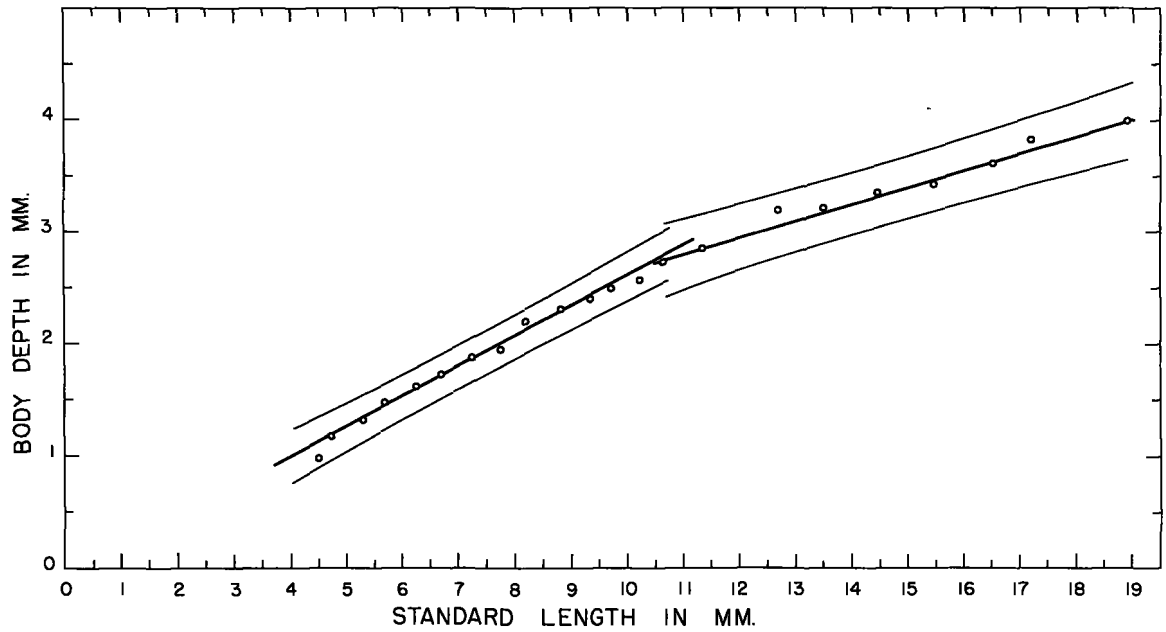

FIGURE 8.—Regressions of body depth (at pectoral) on standard length (middle line of each group). The lines are fitted to the data by the method of least squares, using all measured specimens. One line is for larvae 4.03 to 10.70 mm. in length, the other for larvae 10.67 to 18.90 mm. in length. Each 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.

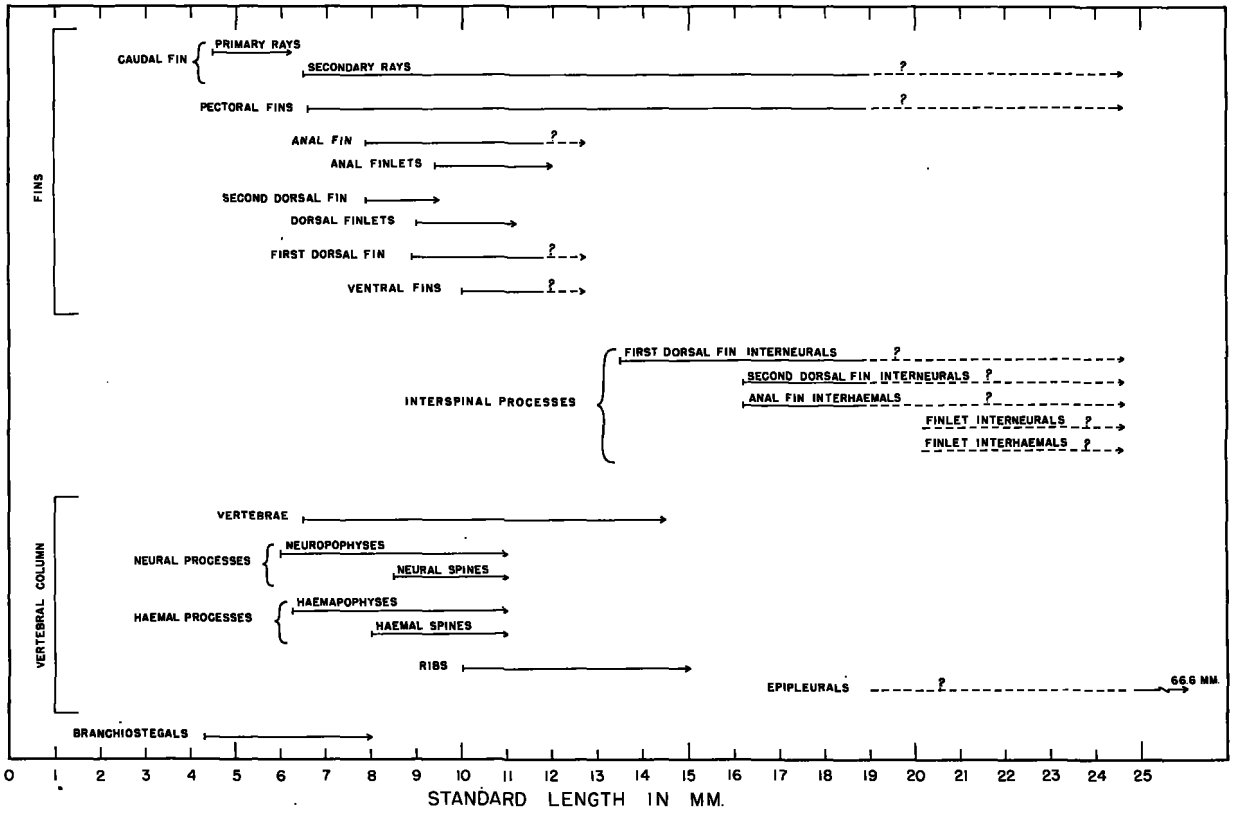

FIGURE 9.—Diagrammatic summary of the sequences of ossification of basic meristic structures and their parts in Pacific mackerel larvae and juveniles. Progressive ossification is indicated by the lines and the symbols attached to them: vertical bars, beginnings of ossification; solid lines, serial growth 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 posterio-ventral to the eyes at about 4.3 mm., and succeeding rays form successively anterioventrad 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
13.5	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, multibranched 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).

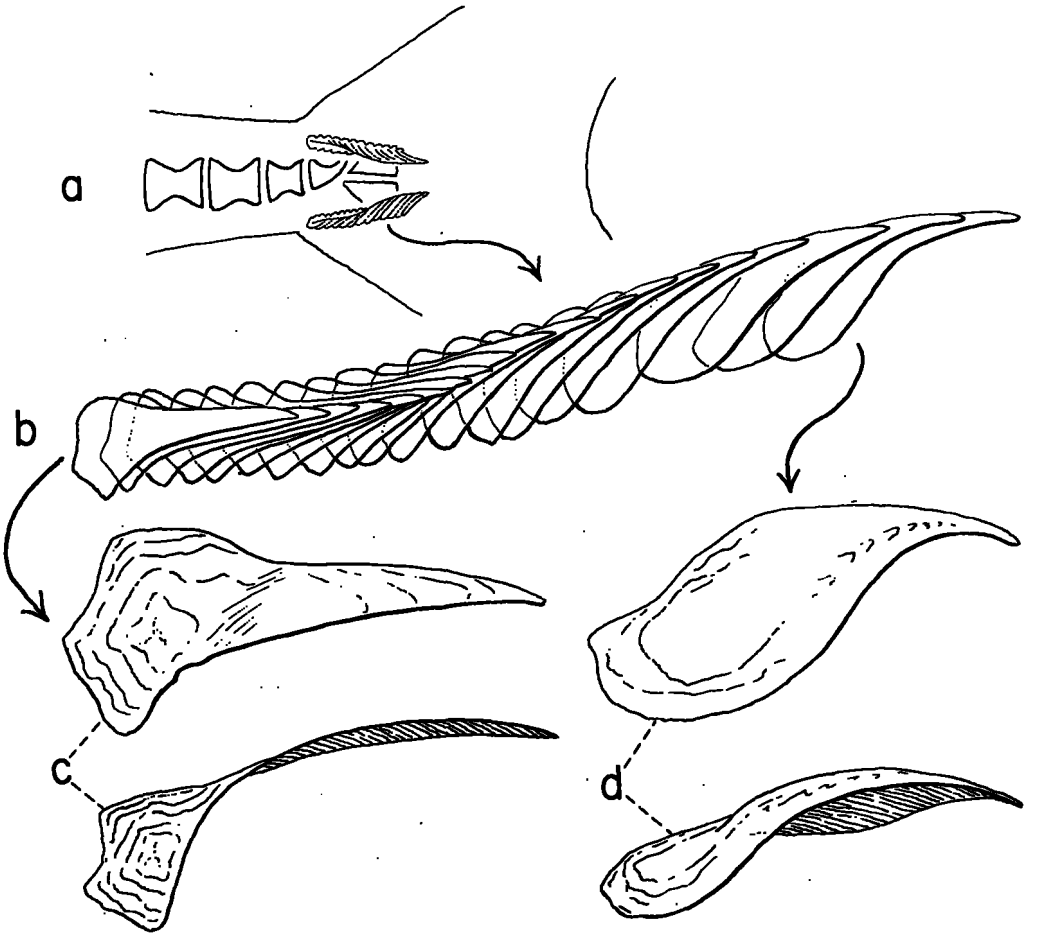

FIGURE 10.—The caudal keels and the scales of the ventral keel on the tail in the Pacific mackerel; from a specimen 66.6 mm. long. *a*. Positions of the keels on the left side of the tail (not accurate for counts). *b*. Detail of the arrangement of the scales on the ventral keel. *c* and *d*. Plane and lateral views of the first and last scales, respectively.

Auxis 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 posterioventral 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 difficulty 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 *Auxis 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 *Auxis*, 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 *Auxis*. 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 alignment. 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 midlength 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

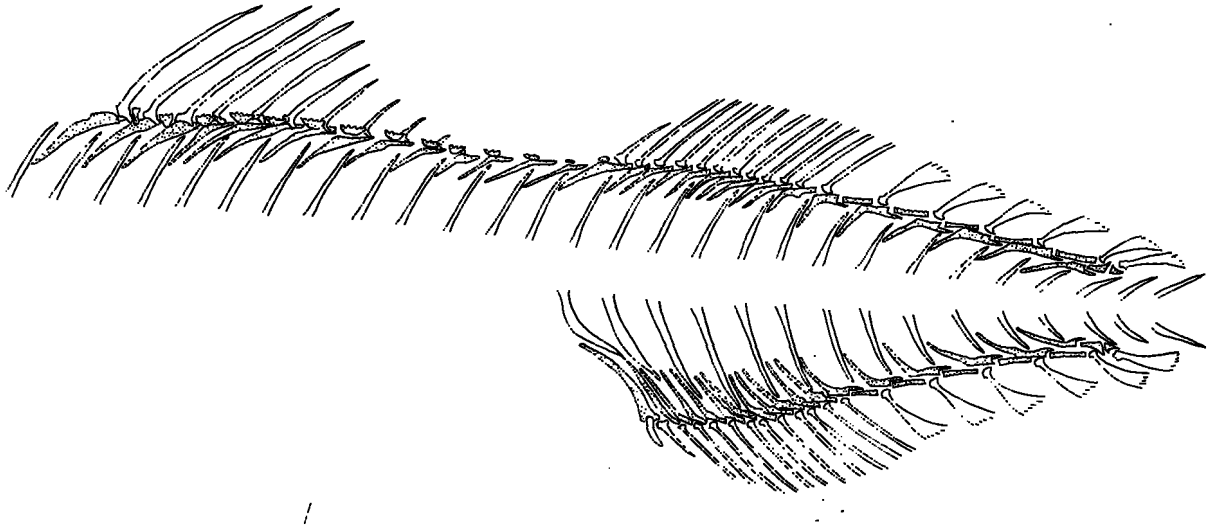

FIGURE 11.—Arrangement of the parts of the dorsal and anal fins and finlets, their interspinal bones and the vertebral spines (2d to 29th neural and 1st to 15th haemal) in the Pacific mackerel; from a specimen 66.6 mm. long (see figs. 12, 13 and 14).

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 *Auxis* 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 neuralspines 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, semitransparent 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.

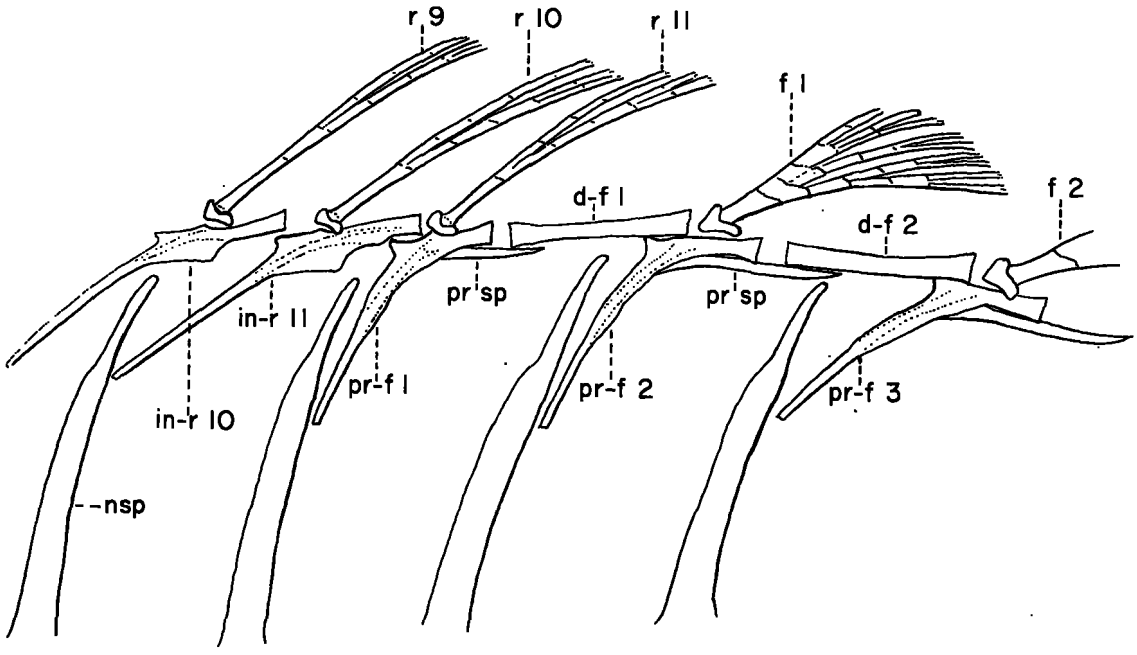

FIGURE 12.—Detailed lateral view of the arrangement of the last three rays of the second dorsal fin, the first two finlets, their interneurals, and the neural spines in the Pacific mackerel; from a specimen 66.6 mm. long (fig. 11); *d–f* 1 and 2, first and second finlets; *in-r* 10 and 11, interneurals of the 10th and 11th rays; *nsp*, neutral 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, nonalate 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).

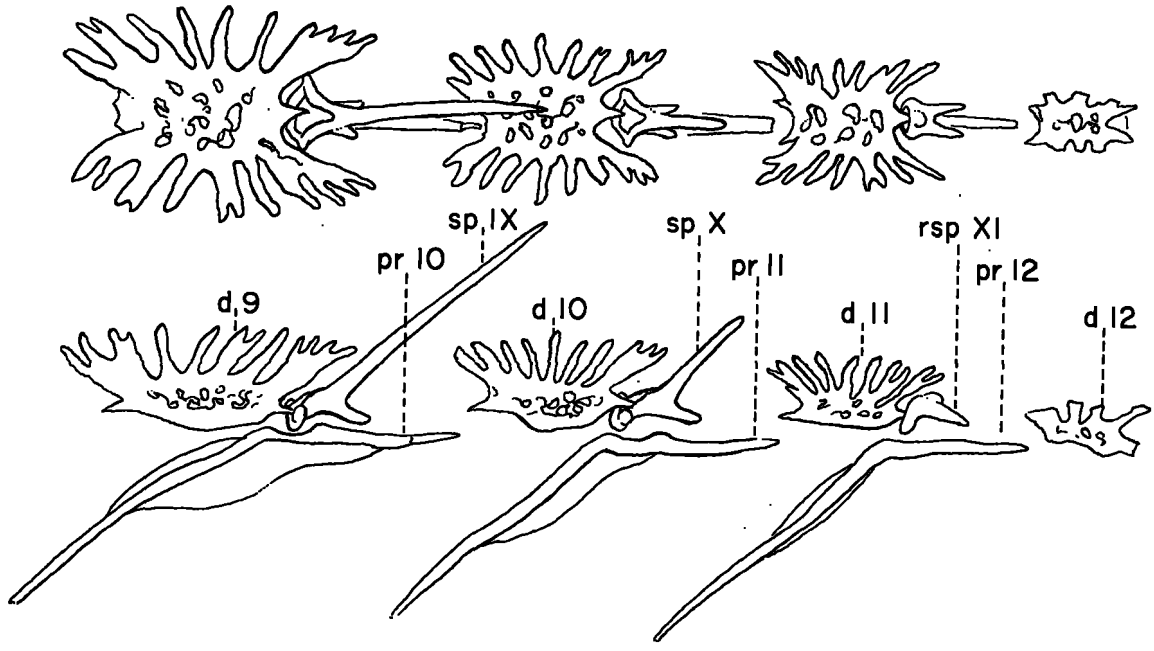

FIGURE 13.—Detailed dorsal and lateral views of the arrangement of the 9th and 10th spines and their interneurals in the first dorsal fin in the Pacific mackerel (also the rudimentary 11th spine): from a specimen 66.6 mm. long (see figs. 11 and 14). *d* 9 through 12, distal sections of the 9th through 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 "baseosts," [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).

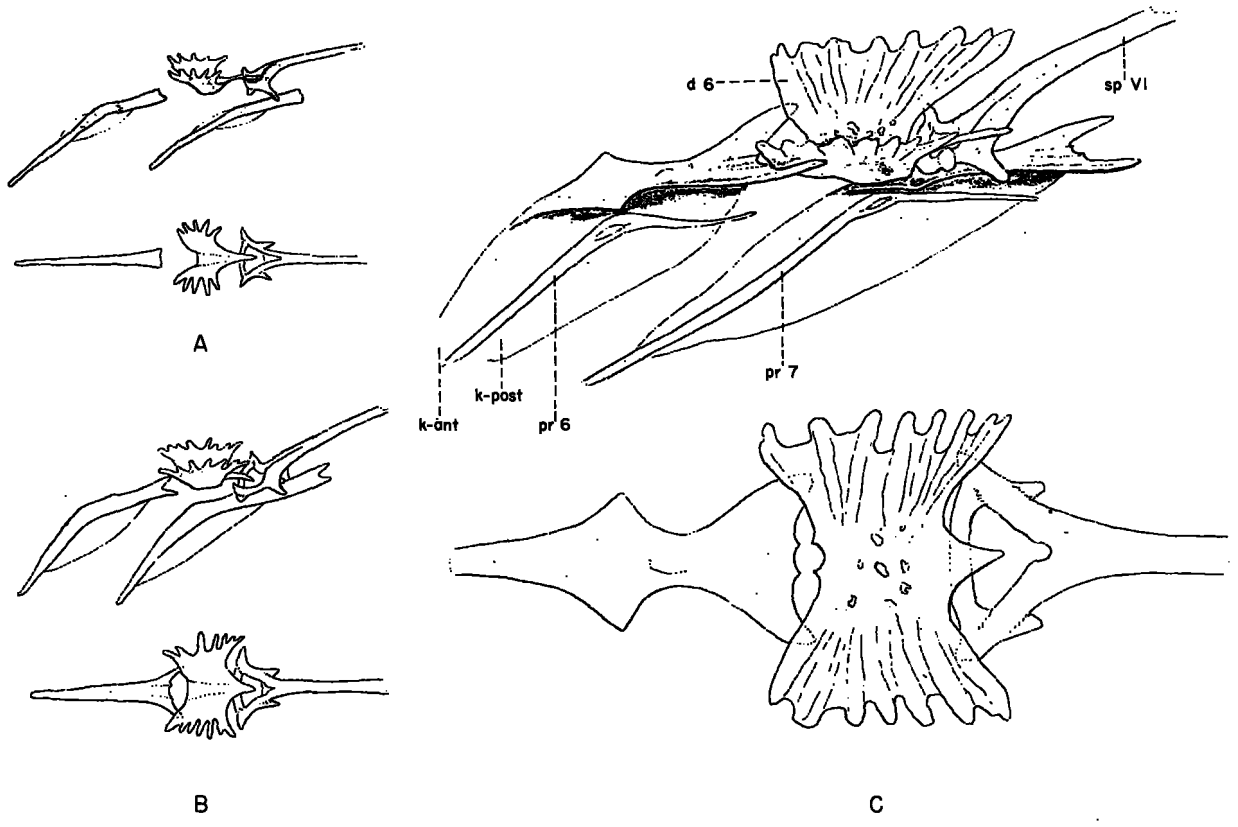

FIGURE 14.—Detailed dorsal and lateral views of the growth of the parts of the interneural of the sixth spine of the first dorsal fin in the Pacific mackerel, illustrating the formation of the dorsal slot (see figs. 11 and 12). *A*, from a specimen 26.4 mm. long. *B*, from a specimen 30.0 mm. long. *C*, 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 "V" 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 *Auxis* species the alate structures are in the same positions on the distal sections of the interneurals as those of the Pacific mackerel. However, 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, *Auxis* 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 *Auxis*.

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 15*a* to *f* and 16*a* 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 posteriorily 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 *Auxis* 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, intially 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

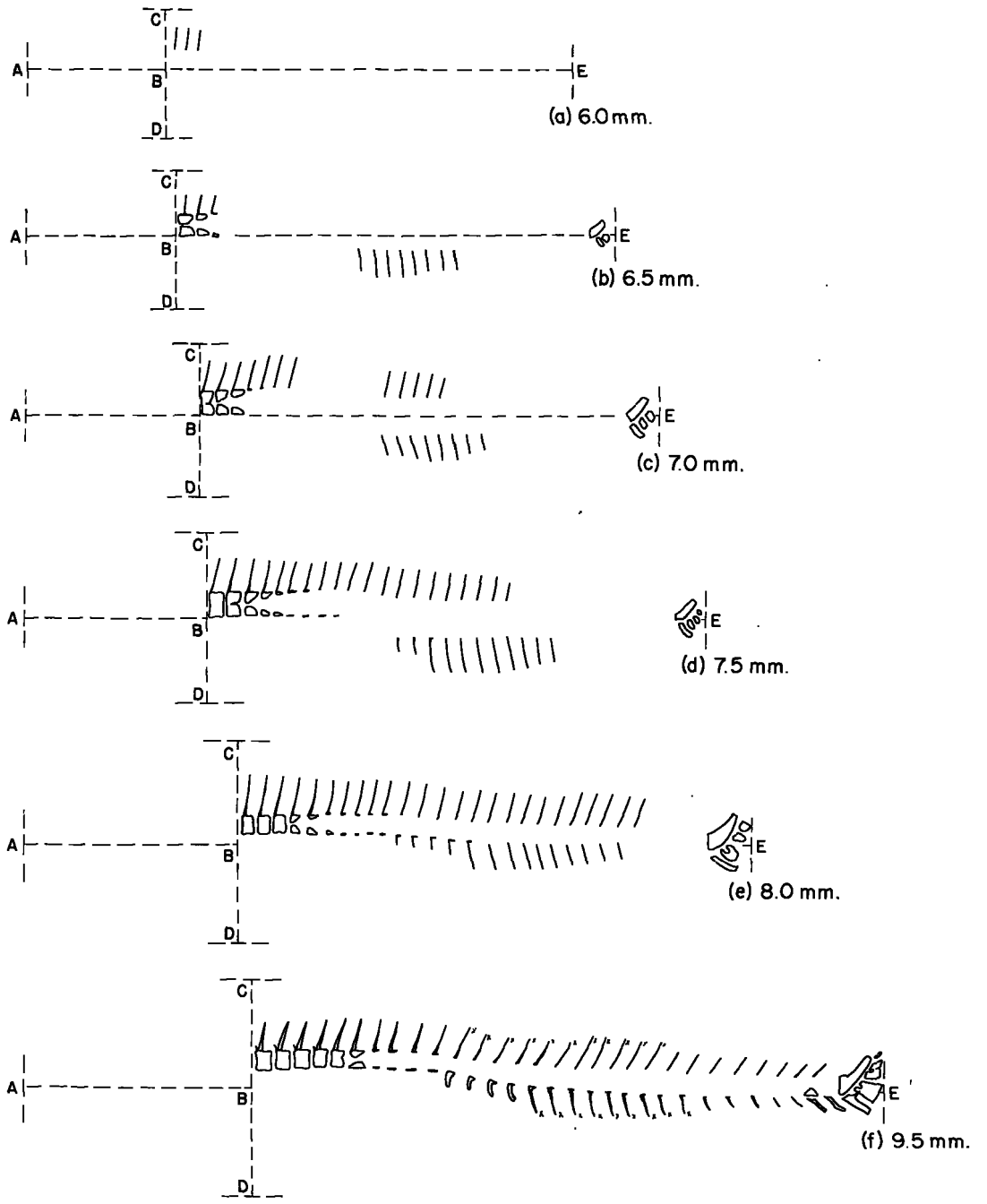

FIGURE 15.—Progressive ossification in the vertebral column in Pacific mackerel larvae from 6.0 to 9.5 mm. in length. The following are drawn to scale: *A-B*, head length; *A-E*, standard length; *C-D*, body depth. The x's on the neural and haemal processes in (*f*) denote fusion of these parts at their 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

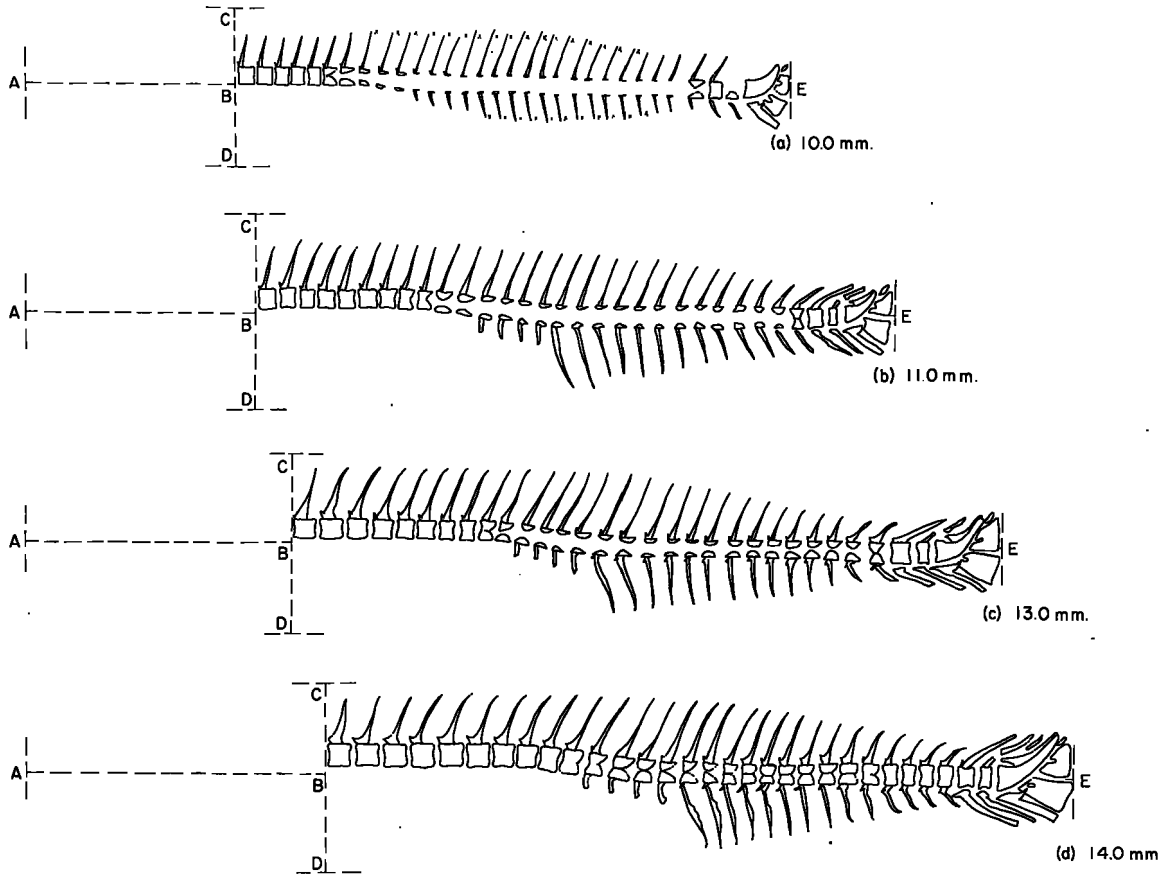

FIGURE 16.—Progressive ossification in the vertebral column in Pacific mackerel larvae from 10.0 to 14.0 mm. in length. The following are drawn to scale: *A-B*, head length; *A-E*, standard length; *C-D*, body depth. The x's on the neural and haemal processes in (*a*) denote fusion of these parts at 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 interspinal 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.

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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.

Epipleurals.—The last processes to form on the vertebrae are the epipleurals, 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 epipleurals 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 epipleurals 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 haemapophyses, 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 zygapophyses 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 vertabrae 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 *Auxis* 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 *Auxis* 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 unknown. 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 Concepcion 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 date 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.

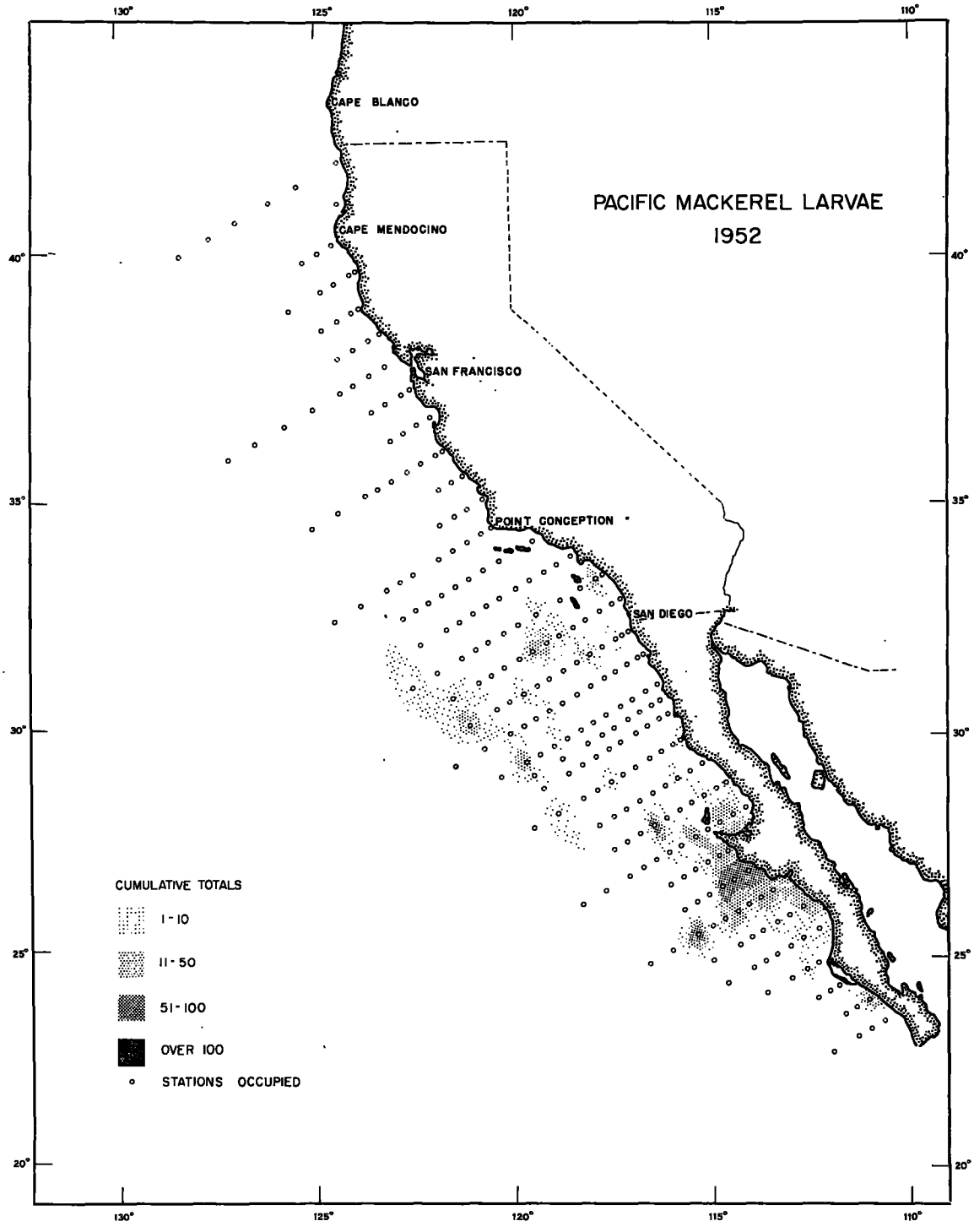

FIGURE 17.—Distribution and abundance of Pacific mackerel larvae in 1952. Cumulative totals represent the summation for the year of the standard haul totals of Pacific mackerel larvae taken at each station on each cruise.

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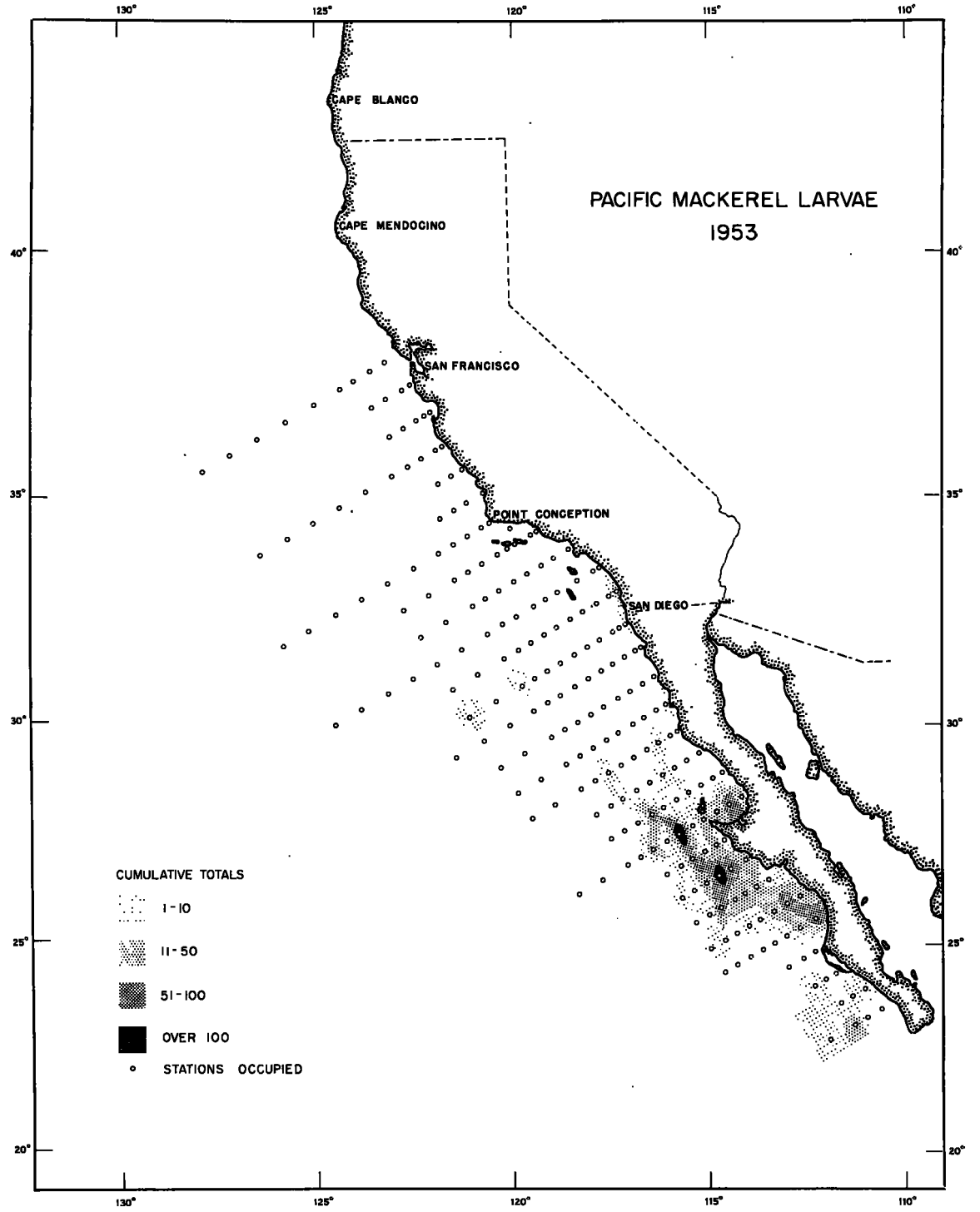

FIGURE 18.—Distribution and abundance of Pacific mackerel larvae in 1953. Cumulative totals represent the summation for the year of the standard haul totals of Pacific mackerel larvae taken at each station on each cruise.

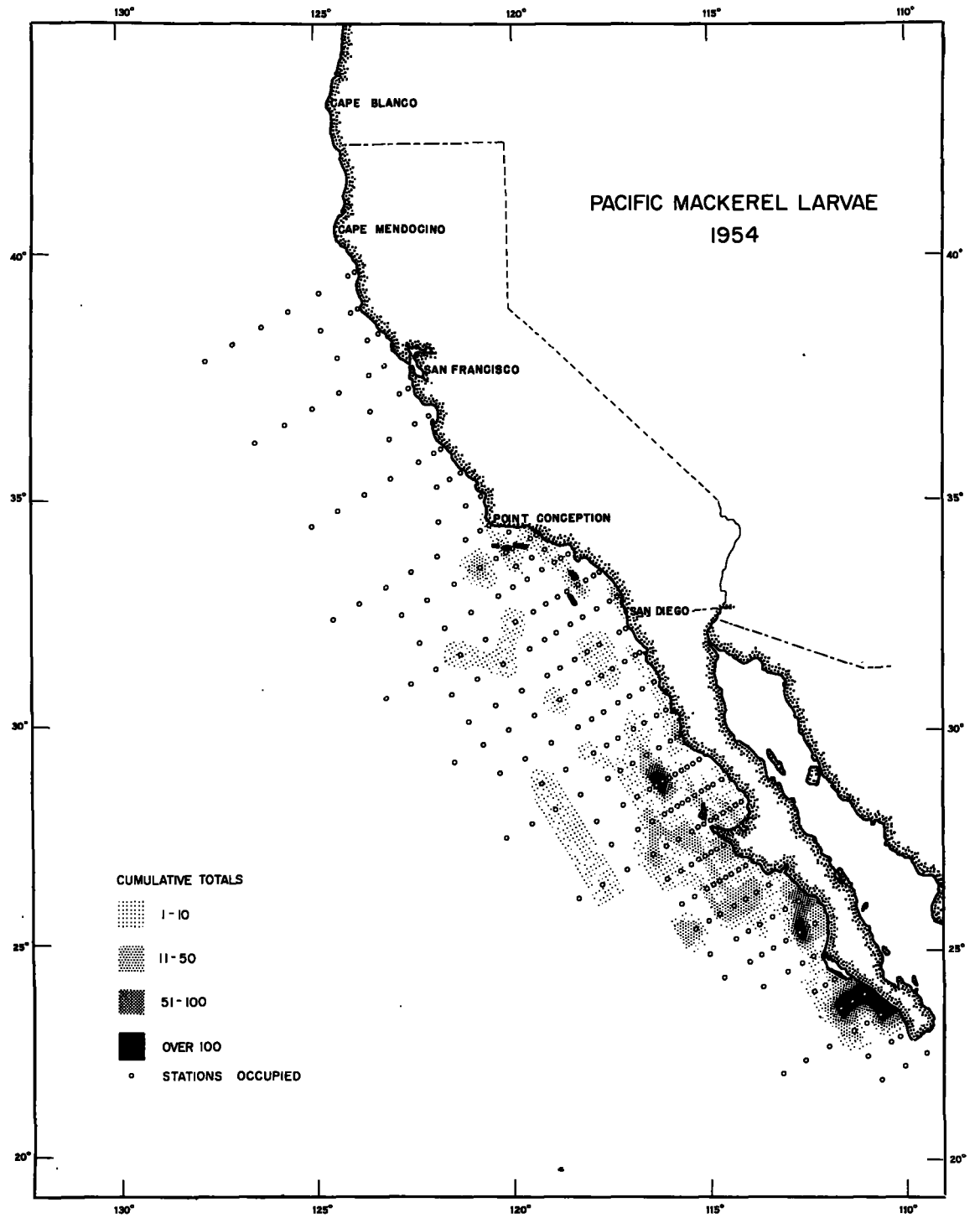

FIGURE 19.—Distribution and abundance of Pacific mackerel larvae in 1954. Cumulative totals represent the summation for the year of the standard haul totals of Pacific mackerel larvae taken at each station on each cruise.

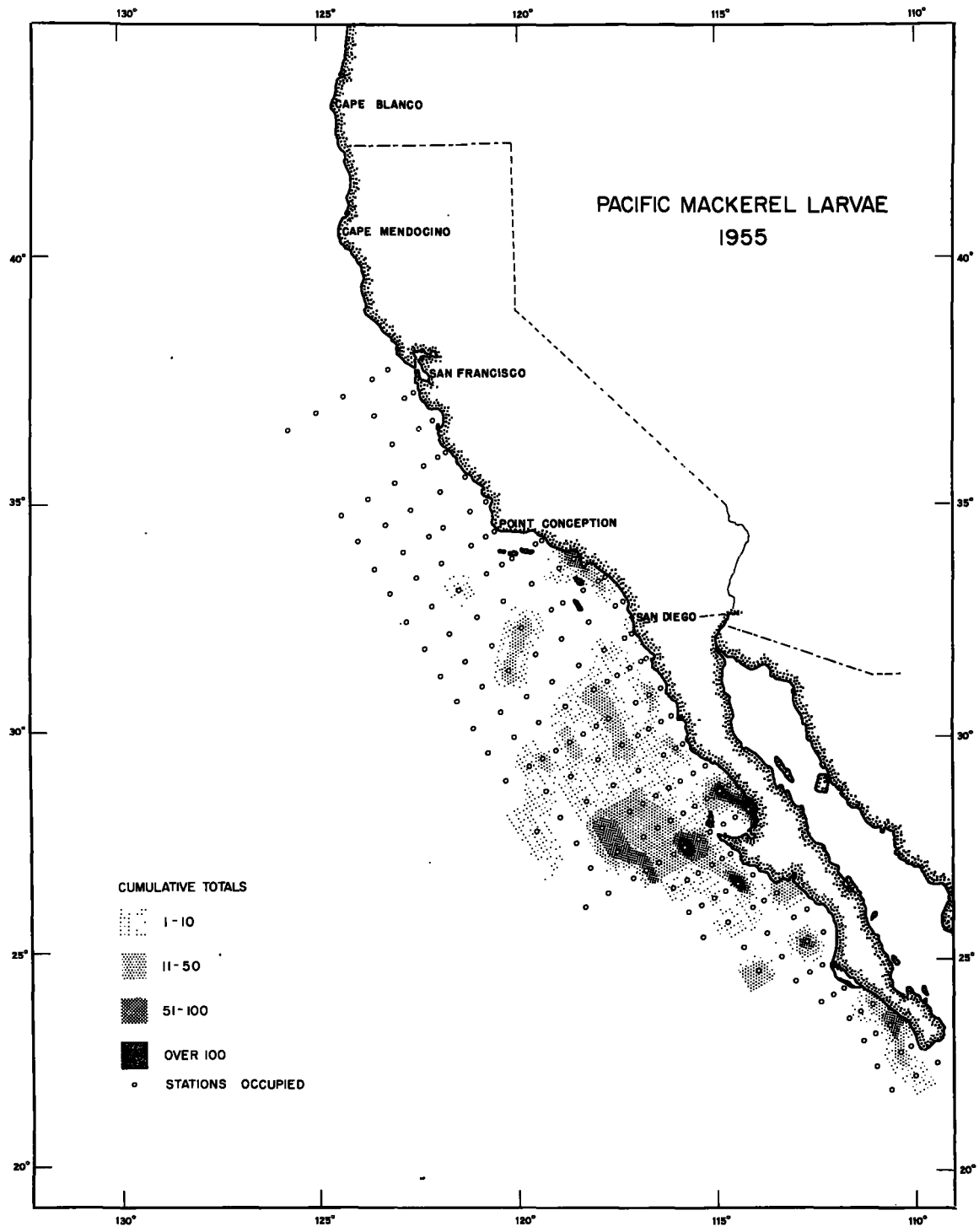

FIGURE 20.—Distribution and abundance of Pacific mackerel larvae in 1955. Cumulative totals represents the summation for the year of the standard haul totals of Pacific mackerel larvae taken at each station on each cruise.

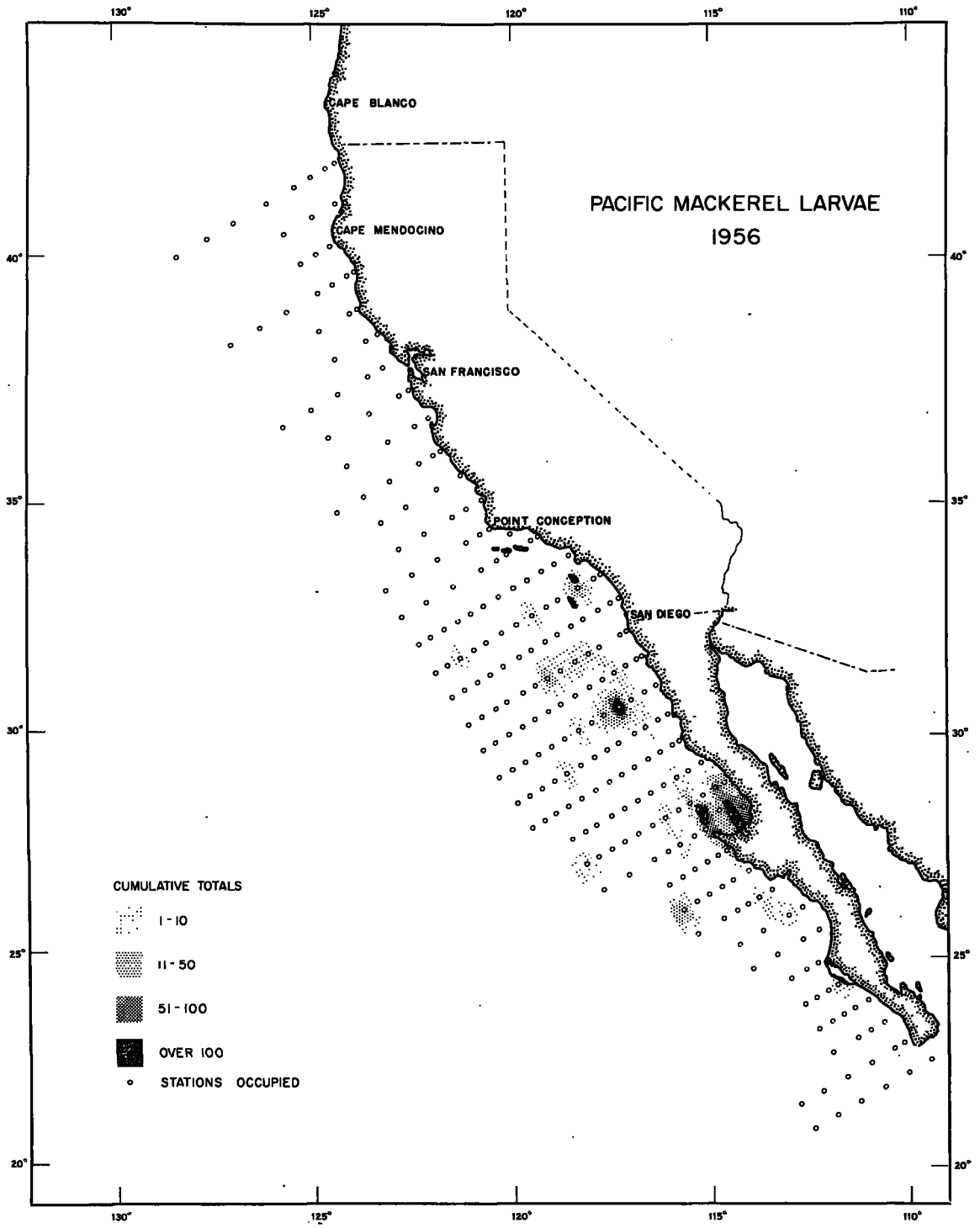

FIGURE 21.—Distribution and abundance of Pacific mackerel larvae in 1956. Cumulative totals represent the summation for the year of the standard haul totals of Pacific mackerel larvae taken at each station on each cruise.

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	[2]0	0	0	0	0		0
80–93	0	0	0		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	0	0	0		.1	0	3.1	0	0	0	0	0	0	3.2
97–107	0	0	0		0	0	4.0	.5	0		1.0		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		0	170.7
123–137	.7	0	8.2	21.0	33.5	57.4	10.3	10.0	62.1		10.6		7.8	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	0	0		0	1.1	10.6	22.4	0		0		0	34.1
97–107	0	0	0		0	3.6	7.3	5.1	1.0		0		0	17.0
110–120	0	0	.5		13.1	22.1	65.8	2.5	34.9		21.0		0	159.9
123–137	38.4	7.7	46.9		5.8	4.9	2.5	29.9	45.9		6.3		3.2	191.5
140–157	373.1												18.9	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	0		0	0	15.9	23.9					0	39.8
97–107	0	0	0		39.4	10.1	4.4	0					0	53.9
110–120	0	0	18.4		170.2	4.0	126.9	23.8					0	343.3
123–137	0	0	46.7		1.7	9.6	42.5	6.3					0	106.8
140–157	54.9	3.5	.6										.7	59.7
Total	54.9	3.5	65.7		211.3	23.7	189.7	54.0					.7	603.5
1956														
60–77					0	[2]0	[2]0	0						0
80–93	0	0	0		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				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 tenth's 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	Number	Percent	Number	Percent	Number	Percent	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*

[Estimates in billions]

Month	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	15.28	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-

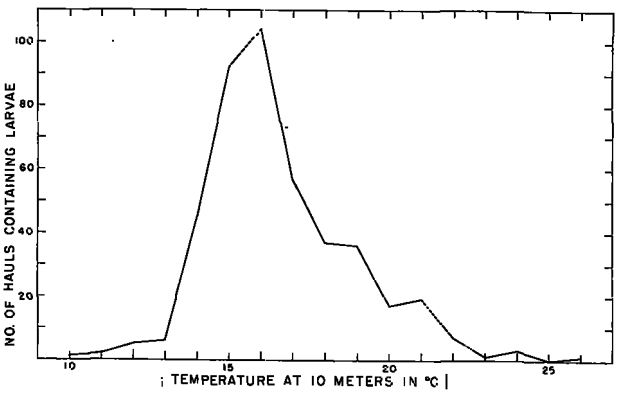

FIGURE 22.—Relation between water temperatures (at 10 meters) and number of hauls containing Pacific mackerel larvae, 1952 through 1956 (see table 10).

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, 1952–56* [1]

Temperature at 10-meter level (° C)	Number of standard hauls that contained—					
	1–10 larvae	11–50 larvae	51–100 larvae	101–200 larvae	More than 200 larvae	Total
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	[1] 16.6	248
Northern central Baja California	113.45	June	1954	[1] 16.3	118
Do	113.47	do	1954	17.3	103
Do	117.30	do	1955	[1] 15.7	349
Do	118.35	August	1956	20.4	468
Do	118.39	July	1956	18.0	159
Do	120.50	April	1955	[1] 15.3	105
Do	120.50	June	1953	[1] 15.9	158
Southern central Baja California	127.40	March	1955	[1] 15.1	129
Do	127.45	May	1953	[1] 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 (bastopore 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 pseudofins 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*

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								
2.30	0.59	0.26	[1] YS	1.07								[2] LB							
2.40		.26	YS	1.20								LB							
2.45	.61	.26	YS	1.22								LB							
2.45	.66	.26	YS	1.20								LB							
2.55	.66	.28	YS	1.17								LB							
2.58		.27	YS	1.22								LB							
2.60	.69	.26	YS	1.25								LB							
2.65	.66	.27	YS	1.16								LB							
2.68	.61	.26	YS	1.25								LB							
2.70	.54	.28	YS	1.02								LB							
2.70	.69	.31	YS	1.17								LB							
2.70	.66	.26	YS	1.25								LB							
2.73	.66	.33	YS	1.02								LB							
2.75	.61	.28	YS	1.25								LB							
2.75		.31	YS	1.28								LB							
2.75	.61	.38	YS	1.25								LB							
2.78	.71	.28	YS	1.15								LB							
2.86	.66	.28	YS	1.12								LB							
2.88	.59	.33	YS	1.02								LB							
2.91	.66	.36	YS	1.33								LB							
2.91	.60	.32	YS	1.26								LB							
2.91	.59	.31	YS	1.02								LB							
2.96	.76	.38	YS	1.43								LB							
2.96	.69	.33	YS	1.20								LB							
2.98	.69	.38	YS	1.22								LB							
3.01	.76	.38	YS	1.43								LB							
3.06	.76	.38	YS	1.53								LB							
3.09	.71	.38	YS	1.45								LB							
3.11	.71	.43	YS	1.40								LB							
3.16	.79	.38	YS	1.43								LB							
3.21	.82	.38	YS	1.53								LB							
3.32	.76	.41	YS	1.43								LB							
3.34	.76	.41	YS	1.43								LB							
3.42	.79	.41	YS	1.58								LB							
3.42	.79	.41	YS	1.61								LB							
3.42	.81	.43	YS	1.58								LB							
3.49	.71	.46	YS	1.58								LB							
3.57	.92	.43	YS	1.71								[3] LP							
3.72	.94	.43	YS	1.71								LP							
4.03	.89	.44	.87	1.81								LP							
4.13	1.02	.48	.97	1.81								LP							
4.18	1.02	.51	1.05	1.89								LP							
4.28	.92	.41	.82	1.78								LP							
4.31	1.12	.54	1.15	2.19				2				LP							
4.38	1.05	.51	1.10	2.12				1				LP							
4.44	.99	.51	.99	2.09								LP							
4.51	1.25	.64	1.15	2.30				4	4			LP							
4.51	1.27	.64	1.35	2.55				4				LP							
4.54	1.25	.59	1.22	2.35				3	4			LP							
4.56	1.17	.56	1.10	2.30				1				LP							
4.56	1.02	.50	.89	2.04								LP							
4.62	1.22	.64	1.20	2.40				3	2			LP							
4.62	1.02	.48	.79	1.94								LP							
4.67	1.33	.64	1.33	2.50				4	8			LP							
4.74	1.15	.54	1.20	2.30				2	2			LP							
4.74	1.28	.64	1.28	2.45				4	4			LP							
4.82	1.15	.51	1.17	2.24				2				LP							
4.84	1.25	.54	1.15	2.30				1				LP							
4.84	1.20	.54	1.17	2.30				1				LP							
4.87	1.20	.59	1.25	2.37				2	4			LP							
4.90	1.22	.51	1.07	2.07								LP							
4.95	1.22	.57	1.17	2.37				4				LP							
4.97	1.22	.56	1.33	2.55				2	2			LP							
5.04	1.25	.61	1.33	2.65								LP							
5.10	1.20	.54	1.15	2.37				1				LP							
5.12	1.22	.54	1.07	2.30								LP							
5.13	1.40	.69	1.48	2.65				5	8			LP							
5.20	1.40	.64	1.43	2.52				3				LP							
5.35	1.28	.54	1.22	2.42				1				LP							
5.36	1.22	.54	1.20	2.55								LP							
5.36	1.35	.64	1.33	2.60								LP							
5.38	1.53	.64	1.45	2.96				5	10			LP							
5.41	1.40	.61	1.35	2.70								LP							
5.41	1.38	.61	1.30	2.75								LP							
5.42	1.33	.59	1.35	2.52				2				LP							
5.47	1.35	.71	1.35	2.62				5	9			LP							
5.48	1.40	.64	1.38	2.68				3				LP							
5.50	1.53	.69	1.53	2.98				5	11			LP							
5.53	1.50	.71	1.53	3.04				5	11			LP							
5.55	1.45	.61	1.40	2.75				5	7			LP							
5.56	1.25	.56	1.10	2.35								LP							
5.56	1.53	.69	1.50	2.93				4				LP							
5.58	1.40	.61	1.35	2.80								LP							
5.58	1.40	.64	1.28	2.70								LP							
5.61	1.48	.69	1.45	2.86				4	9			LP							

See footnotes at end of table.

Measurements and meristic counts of specimens (exclusive of juveniles and adults) of Pneumatophorus diego—Con.

MORPHOMETRIC MEASUREMENTS (mm.)							MERSTIC 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								
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	1.48	.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	1.68	.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	1.40	.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	1.50	.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	1.83	3.90				6	17			LP							
6.38	1.63	.74	1.71	3.62				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				LP							
6.46	1.97	.76	1.77	3.68			14	6	17		1	LP							
6.47	1.98	.89	2.04	3.95			12	6	17			LP							
6.55	1.68	.76	1.68	3.32				5				LP							
6.57	1.98	.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				6	15			LP							
6.62	1.94	.92	1.81	3.82			23	6	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	1.58	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	1.78	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	------	------	------	------	------	------
8.03	2.24	.97	2.32	4.59	------	------	26	6	17	2	2	6	6	------	------	------	------	------	------
8.04	2.37	1.07	2.22	4.74	------	------	25	7	17	2	2	7	------	------	------	------	------	------	------
8.05	2.50	1.02	2.17	4.90	------	------	25	6	17	2	1	6	------	7	------	------	------	------	------
8.05	2.32	1.05	2.27	4.84	------	------	------	7	17	2	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	------	------	------	7	17	1	2	------	------	------	------	------	------	------	------
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	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
8.24	2.04	.94	1.91	4.13	------	------	------	------	------	------	------	------	------	11	------	1	------	------	------
8.24	2.17	.99	2.17	4.59	------	------	21	6	17	------	------	5	5	------	------	------	------	------	------
8.25	2.27	.99	2.17	4.84	------	------	23	7	17	------	------	8	8	------	------	------	------	------	------
8.30	2.37	.94	2.17	4.69	------	------	23	7	17	1	1	------	------	------	------	------	------	------	------
8.35	2.67	1.05	2.22	4.84	------	------	24	7	17	2	2	7	------	------	------	------	------	------	------
8.45	2.77	1.09	2.37	5.09	------	------	31	7	17	3	3	8	9	11	11	4	3	IV	------
8.48	2.50	.99	2.30	5.04	------	------	28	6	17	1	2	7	------	8	7	------	------	------	------
8.67	2.47	1.07	2.22	4.92	------	------	31	7	------	------	------	9	9	I, 11	I, 11	1	------	------	------
8.67	2.17	.92	2.19	4.69	------	------	------	7	17	------	1	------	------	------	------	------	------	------	------
8.77	2.40	1.05	2.30	5.02	------	------	------	7	17	2	2	9	9	9	9	------	------	------	------
8.89	2.72	1.19	2.42	5.63	------	------	------	7	------	------	------	------	------	I, 11	I, 11	4	4	VI	------
8.94	2.67	1.09	2.42	4.99	------	------	25	7	17	2	2	7	7	8	8	------	------	------	------
9.03	2.40	1.02	2.22	4.82	------	------	23	7	17	2	2	7	8	7	8	------	------	------	------
9.09	2.37	.99	2.32	4.89	------	------	23	7	17	2	2	5	6	------	------	------	------	------	------
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	2	2	8	8	10	11	1	1	------	------
9.39	2.67	1.04	2.42	5.14	------	------	25	7	17	3	2	7	8	7	7	------	------	------	------
9.40	2.65	1.10	2.47	5.25	------	------	27	7	17	2	2	8	9	------	------	------	------	------	------
9.43	2.58	1.10	2.52	5.74	------	------	------	7	17	3	3	10	10	11	I, 11	1	------	------	------
9.44	2.67	1.04	2.42	5.28	------	------	31	7	17	2	3	------	------	9	10	1	1	------	------
9.45	2.65	1.10	2.55	5.65	------	------	31	7	17	3	3	9	9	I, 11	I, 11	1	------	------	------
9.48	2.82	1.10	2.52	5.38	------	------	31	7	17	2	2	9	8	9	10	1	1	------	------
9.49	2.52	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	11	1	1	------	------
9.78	2.77	1.08	2.46	5.53	------	------	------	7	17	3	2	------	------	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	1
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	2	2	11	11	I, 11	------	5	------	IX	2
10.70	3.00	1.07	2.75	6.50	------	------	31	7	17	4	4	10	10	------	------	------	------	------	3
11.10	3.15	1.25	2.95	6.60	------	------	31	7	17	3	3	------	10	------	------	------	------	------	------
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	11	I, 11	6½	6½	VIII	I, 3
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	I, 3
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	1
11.76	3.26	1.24	2.72	7.01	4.35	7.61	31	7	17	5	5	10	10	11	I, 11	5	5	VII	I, 4
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	I, 5
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	VIII	I, 5
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	I, 3
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	I, 5
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	I, 5
14.60	4.15	1.45	3.80	9.30	5.70	9.60	31	7	17	7	6	15	------	I, 11	II, 11	6½	6½	X	I, 5
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	I, 5
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	I, 5
15.20	4.25	1.41	3.41	9.40	5.60	------	31	7	17	8	8	17	17	------	II, 11	6½	6½	------	I, 5
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	I, 5
16.00	4.54	1.53	3.21	10.10	5.90	10.30	31	7	17	7	7	16	15	I, 11	II, 11	6½	6½	X	I, 5
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	6½	X	I, 5
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	I, 5
16.80	4.99	1.58	3.72	10.70	6.30	11.00	31	7	17	8	8	17	18	I, 11	II, 11	6½	6½	X	I, 5
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	I, 5
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	I, 5
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	I, 5

*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 differentation of spines or vertebrae (see figs. 15 and 16).

‡Second dorsal, anal, and ventral fins: arabic numeral alone represents early development; no differentation 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 differentation in early stages may not be apparent.

[1] YS, yolk sac larvae. [2] LB, larval bud. [3] LP, larval pectoral. [4] All verterbral counts after 6.4 mm. include the urostyle (see fig. 15).

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