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UNITED STATES DEPARTMENT OF THE INTERIOR, J. A. KRUG, *Secretary*
FISH AND WILDLIFE SERVICE, ALBERT M. DAY, *Director*

STUDIES OF THE PROTOZOAN PARASITES OF FRESH-WATER FISHES

By H. S. DAVIS, Ph. D.

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Studies of the Protozoan Parasites of Fresh-Water Fishes[1]

For a number of years the author has devoted considerable attention to the protozoan parasites of our fresh-water fishes. During the course of these studies it has become apparent that such parasites are more common than was realized and that they include organisms with a wide diversity of form and habits. In fact, all of the major groups of Protozoa are represented although, exclusive of the Myxosporidia which are typically fish parasites, the most common forms belong to a few families of flagellates and ciliates. As might be expected, the degree of parasitism shown by the various forms differs greatly. Some are evidently more or less accidental associates of the fish which may provide support or protection although some inanimate object would probably serve just as well. None of these forms, however, are considered here. Others have become more or less dependent on the fish, but the degree to which they may injure the host varies widely. Some only use the fish for support and protection, while their food is derived exclusively from other sources. Others, even among the external parasites, obtain their nutriment exclusively from the host. Between these two extremes there are many intermediate forms which derive their nourishment from both the host and external sources.

Several species observed during the course of these studies are not included, as the information available is too incomplete to be of value. The species discussed are grouped by orders and families, but further than that, no systematic arrangement has been attempted.

[1] Approved for publication Aug. 6, 1946. Fishery Bulletin 41.

METHODS

In most cases the organisms were studied in both the living and preserved condition. In studying living forms the external parasites were removed directly to the slide and examined in water. Preserved specimens were studied as whole mounts and in sections. For the former, wet smears were prepared by spreading a little of the material on a coverslip which was immediately exposed to osmic vapor for 15 seconds. Then the coverslip was floated face down on a small amount of fixing fluid in a watch glass for about 30 minutes. The fixing fluid was a modification of Worcester's formol-mercuric-acetic mixture prepared as follows:

Saturated solution mercuric chloride	75 cc.
Formalin (formaldehyde 40 percent)	20 cc.
Glacial acetic acid	5 cc.

This fixing fluid has been used almost exclusively and for general use with protozoans is believed to give as good results as any fluid yet devised. Material for sectioning was also fixed in this fluid.

For staining both whole mounts and sections, chief reliance was placed on Heidenhain's iron hematoxylin and Ehrlich's acid hematoxylin using eosin and Bordeaux red as counter stains. A combination of the iron hematoxylin and Ehrlich's hematoxylin techniques was found to be especially valuable for staining trichodinids. For this purpose Ehrlich's hematoxylin solution was substituted for the 0.5 percent solution used in Heidenhain's method. Otherwise, the procedure was the same. When Bordeaux red is used as a counter stain, this method also brings out cilia and flagella very clearly.

Order PROTOMONADINA Blochmann

Family **Bodonidae** Butschli

Colponema agitans n. sp.

[Plate 1, figs. 1–5; plate 8, figs. 88–89]

In the spring of 1942 fingerling crappies (*Pomoxis annularis* and *P. sparoides*) in several ponds at the Fish and Wildlife Service station, Kearneysville, W. Va., were found to be infested with four species of flagellates, all undescribed. The parasites were confined to the gills and sometimes were present in great numbers, although fish from the same pond differed greatly in this respect. In some instances all four species were present, but more often only two or three species were found on the same host. Fish with a severe infection were noticeably emaciated, and smaller and weaker than those less heavily parasitized.

Colponema agitans was the smallest of the flagellates on the gills of the crappies and it also occurred in the greatest numbers. It has also been found on the gills of the bluegill sunfish (*Lepomis macrochirus*). While ordinarily most numerous on the filaments, in several fish it was fully as abundant on the gill rakers, and sometimes occurred, in groups of several hundred individuals, free in the mucus covering the gills. Superficially, it resembles the common fish parasite, *Costia necatrix* and could easily be mistaken for this organism on cursory examination. With our limited knowledge of the Bodonidae and incomplete descriptions of many species, it is difficult to determine the affinities of this organism, but owing to the presence of a wide ventral groove and the arrangement of the flagella, it is placed in the genus *Colponema*, at least, provisionally.

The body of the free-swimming flagellate is pyriform to oval in shape, although it is very plastic and capable of rapid changes in form. When attached to the gills, it often appears triangular (figs. 88 and 89) with the free end forming the base of the triangle. The anterior end is flattened and rounded with a wide, shallow groove which takes a spiral course to the middle of the body (figs. 1–4) where it may lead into a cytostome, although this could not be determined with certainty. There are two flagella, the anterior being about one-half as long as the posterior flagellum. The latter serves as a hold-fast organ to attach the parasite to the gills. Several small refringent granules can usually be seen in the living organism The body is covered with a thin pellicle and in the living organism is 6–8μ long and 3–4.5μ wide. The posterior flagellum is about 10μ in length.

When fixed and stained with iron hematoxylin, the most conspicuous structure is the deeply stained blepharoplast which is usually in the form of a curved rod (figs. 2–5), but rarely may be oval in shape. Owing to the small size of the organism it was difficult to trace the attachment of the flagella to the blepharoplast, but in several instances they appeared to arise from opposite ends of this structure. The position of the blepharoplast in the body showed considerable variation. Usually it was located near the anterior end (figs. 3 and 5), but sometimes was in the middle of the body. The large vesicular nucleus is located in the posterior half of the body and usually contains a rounded karyosome with a layer of chromatin granules attached to the nuclear membrane. In addition to the nucleus and blepharoplast, there may be one or two relatively large, deeply stained granules in the endoplasm.

When an infected gill is placed on a slide, the parasite immediately attempts to free itself by very active, jerky movements which are in striking contrast with those of the other flagellates present. Once free, it swims about rapidly with quick, darting movements.

Bodomonas concava n. g., n. sp.

[Plate 1, figs. 6–14; plate 8, fig. 87]

This flagellate was found on the gills of the crappies (*Pomoxis annularis* and *P. sparoides*) in company with *Colponema agitans*, but differs from the latter species in several important respects. It also occurred in small numbers on the gills of the bluegill sunfish (*Lepomis macrochirus*). This species differs so greatly from other members of the family that it has been necessary to propose a new genus.

The organism is elongate, tapering to a point at the posterior end, while the anterior end is broad, flattened and slightly rounded. One side of the body, especially at the anterior end, is much thinner than the other, thus forming a broad, shallow groove which fades out posteriorly (figs. 11, 13, and 14). When attached to the gills the broad, free anterior end is frequently curved toward the ventral side so that the animal is roughly spoon-shaped (figs. 7 and 10). A clear area can be distinguished in the middle of the anterior end which is probably the

cytopharynx. Two flagella arise from the anterior end, one, which is about as long as the body, projects anteriorly and is usually motionless but may move slowly about like a whiplash. When motionless the free end of the flagellum is frequently curved like a hook (fig. 12). The other flagellum is considerably longer and extends posteriorly. It serves as a holdfast organ to anchor the parasite firmly to the gill epithelium. This flagellum is invisible when the parasite is attached and consequently the organism appears to be anchored to the gills by the pointed posterior end. There is a small contractile vacuole near the anterior end and scattered through the endoplasm are the usual refringent granules or fat globules.

The nucleus and blepharoplast are invisible in the living animal, but can be distinguished easily after staining. The nucleus is located near the middle of the body and contains coarse granules of chromatin attached to the nuclear membrane. Sometimes a karysome can be distinguished. The blepharoplast forms a circular or oval disk-shaped body anterior to the nucleus. It usually stains deeply and uniformly, but occasionally takes only a grayish stain in iron hematoxylin. As mentioned above, one side of the body is much thicker than the other and the nucleus is always located in the thicker side. The blepharoplast, however, may extend into the thinner expanded anterior end.

The length of the organism, exclusive of the flagella is about 12 μ and the width 4.5–5μ.

Unlike the other flagellates with which it was associated, *B. concava* was most numerous at the ends of the filaments and when the gills are first removed to a slide are usually motionless. Later, while still attached, they begin to free themselves by violent wriggling movements and contortions of the body which may give them a very different appearance. Once free from the epithelium, they progress by rapid undulatory movements of the body, resulting in a slow forward motion in which the flagella appear to have no part. The anterior flagellum waves about aimlessly through the water, while the posterior flagelleum is stretched out straight behind.

Family **Trypanosomatidae** Doflein

Lamellasoma bacillaria n. g., n. sp.

[Plate 2, figs. 15–18; plate 8, figs. 90–96]

This remarkable organism was found in company with the two preceding species of flagellates on the gills of fingerling crappies (*Pomoxis annularis* and *P. sparoides*). It occurred on a large percentage of the fish examined and in some instances was the most abundant parasite present.

This parasite closely resembles the blood trypanosomes in shape. The body is flattened and ribbon-like with a bluntly rounded anterior end. It is wider near the middle of the body and then tapers gradually toward the posterior end from which projects a long flagellum. The flagellum is shaped like a whiplash, thicker at the base and tapering gradually toward the tip. The most striking characteristic of the organism is the presence of several rows of small refringent rods running lengthwise of the body (fig. 15). At the anterior end the rods are arranged at an angle to the long axis of the body. There is also a small contractile vacuole in this region. The extreme anterior end is free of rods, very transparent and usually in active movement, changing shape rapidly. Two individuals were observed without the characteristic rods, but these were the only ones out of hundreds examined. The length of the body was about 15–20μ with a width of 3–4μ. The flagellum is considerably longer than the body, reaching a length of 30μ.

The nucleus, blepharoplast and rods stain deeply with iron hematoxylin while the rest of the organism is colorless or only lightly stained. The remarkable arrangement of the rods then becomes clear. They are closely attached to the body throughout their entire length and usually appear to be at least partially embedded in the ectoplasm. However, owing to the small size of the parasite, this is difficult to determine with certainty. In sectioned material the rod may be wholly or partially dislodged from the body. They are ordinarily present on both sides of the body, although they have a more uniform arrangement on one side where they always occur in parallel rows arranged end to end as shown in the figures. Six to eight rows can usually be distinguished in the middle of the body, although in small individuals the number may be less. On the opposite side the rods not only form a less regular pattern, but are fewer in number and sometimes may be absent altogether. These rods are probably bacteria, but how they become arranged in such a remarkable manner is difficult to understand. Furthermore, they are more refractive than ordinary bacteria. Of course, bacteria are known to occur on the bodies of many protozoans, but such a regular arrangement is very exceptional, to say the least.

The nucleus is located about one-third the distance

from the anterior end. It is rounded or oval with several large masses of chromatin attached to the inner side of the membrane. A rounded karyosome may also be present. Anterior to the nucleus is a somewhat longer oval blepharoplast which stains even more intensely than the nucleus. In the region of the nucleus and blepharoplast the body is thicker than elsewhere, but becomes thinner toward the opposite edge where it is extended into a transparent membrane. This membrane is bordered by the flagellum which arises from the blepharoplast and extends along the membrane the entire length of the body.

When attached to the gills the parasite has a very different appearance than in the free-swimming condition described above. At this time it is saucer-shaped and closely applied to the rounded surface of an epithelial cell (figs. 91–93). When an infested gill is first mounted on a slide, the parasite appears as a granular, crescent-shaped body at the outer end of an epithelial cell. It is motionless at first and consequently may be easily overlooked. Sooner or later, however, it begins to squirm about, rapidly elongates and becomes free-swimming. In the attached stage the nucleus and blepharoeplast are close together at one side which is considerably thicker (fig. 92). The flagellum cannot be distinguished except in some instances near its attachment to the blepharoplast. The bacteria show the same linear pattern as in the expanded form, but the arrangement is less regular. There are always a considerable number of parasites that remain attached to the epithelial cells until they disintegrate which suggests the possibility that the organisms can become free-swimming only at a certain stage in the life cycle, but for the present this must remain pure conjecture. Reproduction has not been observed except possibly in one doubtful case which could be interpreted as fission in the attached stage.

In the free-swimming stage the organism moves slowly about with the flattened surface uppermost. It progresses by a slow undulatory movement somewhat resembling that of a leech, with the rounded anterior end foremost and the long flagellum trailing motionless in the rear.

Order EUGLENOIDINA Blochmann

Family **Euglenidae** Stein

Euglenosoma branchialis n. g., n. sp.

[Plate 2, figs. 19–23; plate 8, figs. 97 and 98]

This is the fourth species of flagellate found on the gills of the crappie (*Pomoxis annularis* and *P. sparoides*). Unfortunately, the parasite was not recognized at the time the fish were collected and, consequently, only preserved material in the form of wet smears and sections has been available for study. The organism was found on several fish, but was not abundant in any case and was greatly outnumbered by the other flagellates present. Later efforts to find this parasite have proved fruitless.

The body is distinctly of the euglenoid type, being long, spindle-shaped and tapering to a sharp point at the posterior end. Although covered with a thin transparent pellicle the body is very plastic and capable of great changes in shape. The anterior end is spatulate and apparently very flexible. The ventral side bears a groove which can be deepened by the sides being raised and folded inwards. This groove leads into the cytostome from which arise two flagella of approximately equal length (fig. 23). Neither flaggelum appears to extend in any particular direction. They are attached to a small, rounded blepharoplast located on the dorsal side of the cytopharynx. Anterior to the blepharoplast is a small, deeply stained granule which is probably the stigma. The ventral groove widens posterior to the cytostome and the entire body is twisted spirally (figs. 19 and 20). Sometimes this flattening and twisting of the body is quite pronounced, in other individuals it may be scarcely noticeable.

The internal structure is frequently difficult to make out, owing to the large amount of deeply-stained material. Except at the extreme anterior end, the endoplasm is strongly vacuolated and coarsely granular. In addition to the nucleus there are one or more rounded bodies composed of granules staining with iron hematoxylin embedded in an unstained matrix (fig. 23). It is possible that these are paramylum bodies. The oval nucleus is located near the middle of the body, and contains a large oval endosome and a layer of chromatin granules on the inner surface of the membrane (fig. 21). Occa-

sionally in wet smears the nucleus fails to stain with iron hematoxylin and has a uniform grayish color (fig. 23). The length of the fully extended organism ranges from 20 to 30μ with a width of 4–5μ.

When attached to the gills the animal has a very different appearance (fig. 22) and in fact, is scarcely recognizable as the same organism. It is contracted into a rounded disk, shaped like a lozenge. In some cases the anterior end can be distinguished at one side and the same internal structures are present, but with a different arrangement. In a few instances the organism was located in a shallow depression, but usually it appeared to lie in contact with the unmodified epithelium possibly held in place by the flagella.

The exact relation of this organism to the host is uncertain. When first noticed, it was thought that its presence was purely accidental, but after further study, it becme evident that it was as truly an inhabitant of the gills as the other flagellates. This is clearly indicated by the fact that it occurred in considerable numbers on one fish, while absent on others collected at the same time. The fact that it assumes a very different form when attached to the gills also lends strong support for the same conclusion. This, of course, does not necessarily mean that it is a true parasite, the evidence for which is inconclusive. There was no evidence of injury to the gills, but this could hardly be expected of an organism present in such small numbers. The same is true to a large extent of the other flagellate-present, yet fish with a heavy infection were definitely weakened.

Order HOLOTRICHA Stein

Family **Amphileptidae** Schouteden

Amphileptus voracus n. sp.

[Plate 2, figs. 24–26; plate 8, figs. 99–108]

This interesting ciliate was found on the gills of fishes, from the Mississippi River at Fairport, Iowa, which had been sectioned for studies on Myxosporidia. The fishes infected included the carp sucker (*Carpiodes carpio*), the smallmouth buffalo (*Ictiobus bubalus*), and the channel catfish (*Ictalurus punctatus*) Later, the same organism was found on the gills of the pearl minnow (*Margariscus margarita*) at Kearneysville, W. Va. The ciliate was not common in any instance and the author's observations have been confined almost entirely to sectioned material. Only two or three living specimens have been seen and these died in a short time.

In general, this ciliate resembles a parasite, *Amphileptus branchiarum*, of the gills of tadpoles, which was described by Wenrich [2] (1924), but differs from it in several important respects. It is possible that the differences are sufficient to justify the erection of a new genus, but until our knowledge of these organisms is more extensive, it is believed that nothing would be gained by such action. While the ciliate may swim about freely, it appears that during most of its existence it is attached to the gills of some fish. It is always located in a depression in the gill epithelium which is evidently the result of its own activities. Sometimes the organisms may be almost entirely surrounded by epithelial cells (fig. 99), but frequently the depression is quite shallow (fig. 102). Ordinarily there is no covering over the open side of the concavity, but sometimes this may be closed by a thin membrane which appears to be continuous with the cuticle of the epithelial cells.

MORPHOLOGY

Amphileptus voracus is ovoid—sometimes nearly spherical—in shape and covered with a thin pellicle showing parallel striations formed by alternating ridges and furrows. It has not been possible to follow the exact course of these striations, but apparently they are transverse to the long axis over about two-thirds of the body and then turn abruptly at right angles to their former course. Rows of long delicate cilia arise from the furrows between the concentric ridges and each ridge contains a single row of trichocysts (figs. 106 and 108). There is no evidence of flattening on one side of the body as in other species of *Amphileptus*.

The mouth or cytostome is a long crescentic slit near the anterior end and extends about two-thirds the distance around the body. The posterior lip of the cytostome is formed by a ridge parallel with the other transverse ridges. This lip bears a row of long cilia and there is some evidence

[2] Publications referred to parenthetically by date are listed in Literature Cited.

that in the living animal they may be united to form a membranelle. The rounded anterior end of the body, forward of the mouth, is smooth without either ridges or cilia. In some individuals this region was cone-shaped rather than rounded. Posterior to the mouth the entire body is covered with concentric ridges and ciliated furrows which are progressively less pronounced toward the posterior end.

Long slender trichites extend into the body from the mouth (fig. 24), but no evidence of a cytopharynx could be distinguished. One or more large food vacuoles containing the partially digested remains of ingested protozoans, such as *Trichodina*, were often present. Rounded metaplastic bodies are usually distributed through the endoplasm and are sometimes so abundant as to hide most of the other structures. Two large oval to spherical macronuclei are always present. They are located in the posterior half of the body; are identical in size and appearance; and filled with fine chromatic granules. There is only one micronucleus which lies close to the end of one of the macronuclei (figs. 26 and 101). Frequently no micronucleus can be found and it is possible that in such cases it is so closely attached to the macronucleus as to be indistinguishable. The micronucleus has the usual structure, with a central spherical body or karyosome composed of fine chomatin granules embedded in a homogeneous matrix and surrounded by a clear zone between it and the nuclear membrane. There are a number of small contractile vacuoles near the surface of the body, each with a separate opening to the exterior.

There was great variation in the size of the organism. This was especially noticeable among individuals on the gills of the catfish, some being several times the size of others. Ten individuals in sections ranged from 22 by 25μ to 45 by 45μ, the majority being about 35 by 40μ.

REPRODUCTION

Amphileptus voracus multiplies by binary fission. The first stage in the process appears to be division of the micronucleus which is followed by division of the organism into two daughter cells of equal size. Each contains a macronucleus with a micronucleus at one end. The macronucleus, which is already noticeably elongated, then divides by amitosis (figs. 103 and 104). In this process a lighter zone appears in the middle of the macronucleus and gradually becomes more pronounced as the ends of the nucleus separate. Wenrich found that in *A. branchiarum* the organism is always enclosed in a capsule during fission. It has been impossible to determine if this is the case in *A. voracus*, but in any event it is evident that the daughter cells quickly separate after fission, as it is rare to find two individuals in close contact. No evidence of sexual reproduction was observed.

REMARKS

The relation of *Amphileptus voracus* to the host presents an interesting problem. As shown by Wenrich there is no doubt that *A. branchiarum* is a true parasite since it feeds on the cells of the host. In the present species, however, the situation is very different. While it is possible that the organism may at times feed on epithelial cells, there is no evidence that this is the case. On the contrary it appears that *A. voracus* ordinarily feeds on other protozoans. Whether these are always parasitic it is impossible to say, but there is apparently no reason why they may not prey on nonparasitic forms if they are available. It happens, however, that the gills of all fish harboring *A. voracus* were at the same time infected with one or more species of *Trichodina* or of *Chilodon*. When Trichodina were abundant, *A. voracus* was evidently preying on them to the exclusion of other organisms and a large proportion of those observed contained partially digested remains of trichodinids (fig. 100). Sometimes the diameter of the trichodinid was greater than that of *A. voracus*, indicating that the mouth must be capable of great distension. However, when *Chilodon* was the common parasite, individuals of *A. voracus* present preyed on them with equal unanimity. When this organism is present in any numbers, it must be highly beneficial to the host in freeing it from other protozoans so that the relationship appears to be a true case of commensalism.

Although *A. voracus* must injure the host to some extent in producing the cavity in which it lies, such injuries are slight and not to be compared with the benefits which the fish derives from the association. This cavity is apparently formed by pushing aside the epithelial cells rather than by destroying them. Here *A. voracus* lies in wait for any unwary protozoan that may come its way. How it is able to capture such a large and unwieldy organism as a trichodinid is not apparent. Possibly the prey is immobilized by toxic action of the trichocysts as maintained by some writers. There is also evidence that the posterior lip of the mouth is extensible and may be thrust out to enfold the prey.

Order PERITRICHA Stein

Family **Urceolariidae** Stein

Trichodina sp.

MORPHOLOGY

In addition to descriptions by earlier writers the structure of *T. renicola* has recently been described in some detail by Mueller (1932) and that of *T. spheroidesi* by Padnos and Nigrelli (1942). Nevertheless, in view of the great complexity of the structure of these organisms, which are among the most highly specialized of all parasitic protozoa, it is believed desirable to give a brief description of the anatomy of *Trichodina* in general. The following account is the result of studies on several species parasitic on fish and an attempt has been made to give a composite picture of the structure of trichodinids.

In general the body of a trichodinid is saucer- or bell-shaped, the convex side being ordinarily referred to as anterior and the concave side as posterior. However, these terms when applied to radially symmetrical animals such as the trichodinids are confusing and it is believed more logical to refer to the convex (anterior) surface as adoral, since it contains the opening of the cytopharynx, and to the concave (posterior) surface as aboral. In some species the adoral side may be only slightly elevated while in others it may be dome-shaped or even conical. Moreover, there is considerable variation in this respect among individuals of the same species. The aboral side forms a complicated attachment organ known as the adhesive disk (figs. 109–116). Some writers have used the term "sucking disk," but there is little evidence that the organ is capable of exerting suction and the term adhesive disk is believed to be more in accord with the facts. Encircling the body of the animal just above the adhesive disk is a band of long cilia, forming the ciliary girdle, which is the principal organ of locomotion.

The adhesive disk is the most prominent part of the organism and is composed of a very complicated skeletal structure arranged in the form of three concentric rings. The inner and most conspicuous is the denticulate ring or corona which is made up of a series of horny elements or denticles arranged like beads in a necklace (figs. 53, 54, and 125). Each denticle is shaped like a hollow cone with the smaller end of the cone inserted into the cavity of the adjacent denticle, an arrangement admirably adapted to give both flexibility and strength to the ring as a whole. On the outer side toward the circumference of the disk each denticle bears a flattened, blade-like structure, the hook, which is usually concave on one edge and convex on the other. The concave side is thicker and stains more intensely, while the convex side thins out and is sometimes difficult to distinguish from the surrounding cytoplasm. On the inner side of the denticle and approximately opposite the hook is a short tooth-like process, the ray, which projects toward the center of the disk. There is great variation in the number and shape of the denticles, and for that reason they are of special value in differentiating between the various species. The denticulate ring is located on the surface of the disk and is covered only by a thin, transparent, membrane. Although the rays vary greatly in length in different species, they never extend entirely across the center of the disk which is filled with granular protoplasm.

Overlapping the hooks on the upper or adoral side and extending toward the outer margin of the disk is a circular ribbon-like structure known as the striated band. When viewed from the surface of the disk this band appears as a series of radiating lines extending from the denticulate ring to near the edge of the disk. In sections it is evident that the lines are formed by long, slender rods which lie just above the hooks and extend for about half their length beyond the ends of these structures. The outer end of each rod is attached to the membrane which covers the surface of the adhesive disk. Like the hooks the number of rods varies, but is constant for each species. At the outer edge of the striated band is a distinct line which separates it from the third and outer ring, the "saum" of German writers which forms the border of the adhesive disk. This border is composed of a thin flexible membrane which is joined to the striated band by an articulation upon which it moves freely. The border membrane is finely striated, but the striations are not continuous with those of the striated band, the number usually being somewhat greater (fig. 109). Just above and anterior to the border membrane is a row of fine cilia that are united for the greater part of their length to form a membranelle. This ring of cilia is difficult to make out and has been overlooked by most investigators. According to Padnos and Nigrelli (1942) it occurs in *T. spheroidesi* and is one of the characters they use to distinguish this species from other marine tri-

chodinids. The writer has found this ring of cilia in all species of *Trichodina* described in this paper and believes that it is of universal occurrence. It is, however, more easily distinguished in some species than in others and sometimes can be made out only in cross sections.

A marginal fold of granular cytoplasm known as the velum (figs. 36–42) forms the outer edge or rim of the body proper. The shape and thickness of the velum varies greatly, even in the individuals of the same species, and sometimes it appears to be practically nonexistent (fig. 50)[3]. At the base of the velum there may be several folds or wrinkles between it and the central, more elevated portion of the adoral surface (figs. 36–38 and 46–48). The presence of these wrinkles depends largely on the condition of the adhesive disk. When it is curved downwards, they tend to disappear. Underneath the velum is a shallow groove to which is attached a band of long cilia, forming the so-called ciliary girdle. The structure of the ciliary girdle is difficult to make out, but as described by Wallengren (1897) and Fulton (1923), consists of a series of membranelles, each composed of several cilia which arise from a row of basal granules and unite to form a thin plate. Each membranelle is attached obliquely to the floor of the groove like the teeth on a worm-gear wheel. The membranelles show a tendency to fray out at the ends into their component cilia. The parasite moves about over the body and gills of the host by means of the ciliary girdle which also serves to propel it through the water. When swimming freely, the concave adhesive disk is always in advance in utter disregard of the principles of streamlining.

In some species (*T. fultoni*, *T. discoidea*, *T. platyformis*, *T. vellata*, and *T. tumefaciens*) there is a row of shorter cilia just above the membranelles, which appears to have escaped the attention of previous observers. These cilia, which are very fine and delicate, curve upward past the velum and show a rapid, vibratory movement in striking contrast with the wave-like movement of the membranelles. They are a short distance apart and can best be seen in the living animal when viewed from the adoral surface. It seems probable that these cilia, which will be called marginal cilia, are homologous with the cirri which are characteristic of the genus *Cyclochaeta*.

In *T. myakkae* and *T. symmetrica* it is evident that for each rod in the striated band, there is a corresponding membranelle in the ciliary girdle. While a similar arrangement cannot be demonstrated for other species, there is no reason to believe that this is not the case, but that owing to their larger size, the correspondence in numbers is not so evident. In all species, however, each rod of the striated band is connected with the ciliary girdle by a strand of more deeply staining material (figs. 46–48) and it is assumed that in this way the rods are connected with the corresponding membranelles. Mueller (1938) noted this connection between the rods and ciliary girdle in *Vauchomia* (*Trichodina*) *renicola* and *V. nephritica*. He believed, however, that such a connection was lacking in other species and used this as one of the distinguishing characteristics of the genus *Vauchomia*. On the contrary, the writer has been able to find such a connection in all species of *Trichodina* studied, but it is more easily distinguished in some species than in others. Mueller believed that these structures are myonemes which appears to be a logical assumption. The adhesive disk is very flexible and readily conforms to the contours of the surface to which the organism happens to be attached so that the need of contractile elements is obvious.

The mouth is located at one side of the body just above the velum and opens into the gullet or cytopharynx which extends for some distance into the body (figs. 47 and 52). The cytopharynx bears two parallel rows of long hair-like cilia which follow a spiral course and are continued through the mouth into a groove which also takes a spiral course clockwise around the adoral surface. The character of this spiral band known as the adoral spiral varies greatly in different species. In some, as in *T. myakkae* and *T. symmetrica* it may extend only a little more than half the distance around the adoral surface, while in other species it may make a complete circuit or even more. In either case the adoral spiral contains two rows of cilia which are usually long, but in some cases (*T. fultoni*) may be quite short. Except in the cytopharynx and in the immediate vicinity of the mouth, the cilia of the adoral spiral are usually motionless and instead of being erect are frequently folded over the adoral surface.

Near the center of the body is a large contractile vacuole with a wall composed of modified endoplasm and a duct leading to the exterior. The contractile vacuole is ordinarily described as opening into the cytopharynx, but this is certainly not the case in some species of *Trichodina*. In *T. fultoni*, for example, where on account of its size the duct from the contractile vacuole can be traced easily (figs. 118

[3] It provides a convenient line of demarkation between the adoral and aboral surfaces.

and 127), there is no question that it follows a separate course from the cytopharynx to the surface and opens independently a short distance to the left of the mouth where viewed from the oral surface. Extrusion of liquid from the contractile vacuole through a separate opening has also been observed in the living animal. A similar conditon can be easily demonstrated in *T. platyformis* and *T. tumefaciens* (fig. 147). It is possible that the species differ in this respect, but the writer has been unable to find a clear case of a connection with the cytopharynx.

The most conspicuous object in the endoplasm is the large, horseshoe-shaped macronucleus which is so located that the cytopharynx and the duct leading from the contractile vacuole lie between the open ends of the horseshoe. The macronucleus is filled with finely granular chromatic material with occasional rounded bodies of denser material. The micronucleus is small, rounded, or more commonly ovoid and sometimes greatly elongated. It is located near the open ends of the macronucleus and frequently lies in a shallow depression on the outside of one arm (fig. 57). The micronucleus, as in other ciliates, contains a deeply staining central body separated from the delicate membrane by a clear area. The remainder of the endoplasm is filled with food vacuoles in different stages of digestion, granular material, and fat globules.

REPRODUCTION

Binary Fission

As in other ciliates, the principal method of multiplication in *Trichodina* is by binary fission. As might be expected in an animal of such complexity, the process is by no means a simple one. Nevertheless, it takes place while the organism is moving about as usual and there is no evidence of an encysted or resting stage. Fission has been described in detail by several writers the most recent accounts being by Diller (1928) and by Padnos and Nigrelli (1942). The writer's observations are in essential agreement with those of these investigators.

One of the first indications of fission is a change in the macronucleus, which loses its horseshoe shape and becomes shorter and thicker. At the same time, the velum becomes thickened and the margin somewhat irregular or even crenated in some species. This is accompanied by the appearance of slight indentations in the velum and adoral side which mark the beginning of the constriction that will eventually divide the organism into two equal parts. While these changes are taking place, breaks appear in the striated band immediately beneath the indentations in the velum (figs. 170 and 176), which eventually extend to the denticulate ring. As the macronucleus becomes shortened, the micronucleus moves to one side of the body and divides by mitosis, the plane of division coinciding with that which divides the ciliate into two equal parts (fig. 177). Division of the macronucleus which lags somewhat behind that of the micronucleus is accomplished by amitosis, the nucleus becoming dumb-bell shaped and gradually separating into two equal parts in the usual way.

The two daughter individuals resulting from fission (figs. 171 and 172) are identical with the parent except that they are only one-half the size and contain only one-half the number of skeletal parts. Padnos and Nigrelli found that in *T. spheroidesi* the adoral and aboral bands of cilia were retained, but that the cytopharynx disappeared during fission. The contractile vacuole apparently divided with the macronucleus. This appeared to be the sequence of events in the species observed by the writer.

The skeleton is restored to normal after fission by a complicated process which is initiated when the ciliate first starts to divide. At the time the macronucleus contracts in preparation for division, a series of thin, overlapping plates appear on the lower (aboral) side of the striated band just outside the hooks of the denticulate ring (figs. 170 and 176). After fission is completed, these plates rapidly enlarge and each developes into a denticle similar to those in the original denticulate ring the hooks being formed first and later the rays (figs. 173–176 and 179–181). At the same time the old denticulate ring is gradually absorbed and eventually disappears entirely. Since the number of plates which develop into denticles in each daughter ciliate is twice that of the number of denticles derived from the parent, the original number is thus restored. Furthermore, since the striated band is also divided in half during fission, it is obvious that the number of rods in the band is reduced accordingly. The original number, however, is restored, not by the formation of a new striated band, but by the formation of new rods between those of the original band. In this process a faint line appears between each two striations (figs. 110, 113, and 114) which gradually increases in density until it is indistinguishable from the older striations on either side. Since the new rods develop gradually, the appearance of the new striations provides a convenient means of determining the relative age of trichodinids.

Conjugation

Sexual reproduction by conjugation has been observed by several investigators, but only recently has the process been described in any detail. Contrary to general belief, conjugation is by no means rare and the writer has observed it in 8 of the 11 species considered in this paper. It is probable that failure to find conjugation in the other 3 species was due to the fact that only a limited amount of material was available for study.

A detailed account of conjugation in *Trichodina spheroidesi*, a parasite of marine fishes, is given by Padnos and Nigrelli (1942) although they failed to observe some stages of the process. According to these writers, conjugation in *T. spheroidesi* is anisogamous and the aboral surface of the microconjugant is fitted over the adoral surface of the macroconjugant. The micronucleus of each then begins to swell and eventually divides mitotically. At the same time the macronucleus shows signs of vacuolization and breaks down into large, coarse fragments. These continue to break up into smaller and smaller parts until minute spherical bodies with deeply staining granules are formed. Padnos and Nigrelli were unable to follow changes in the micronucleus immediately preceding the metaphase, the latter, however, was well defined. During the final fragmentation of the macronucleus, two micronuclear divisions take place in each conjugant. Following division of the micronuclei, the protoplasm of the two conjugants becomes continuous and the contents of the smaller individual passes into the larger. The investigators assume that the gametic nuclei then unite to form the synkaryon and the remaining nuclei are resorbed. The ensuing processes are confined to the single large exconjugant.

The exconjugant now contains only one functional nucleus, the synkaryon, and remains of the broken down macronucleus and degenerating micronuclei. Padnos and Nigrelli assume that the zygotic nucleus divides three times, resulting in the formation of eight micronuclei. Seven of these become macronuclear anlagen and one the functional micronucleus. The latter divides in the usual way and in the division of the cell the macronuclear anlagen are distributed between the daughter cells. The most frequent distribution is three and four, but sometimes may be two and five or even one and six. In any case, cell division continues until each of the daughter individuals contains one macronuclear anlage and a micronucleus. The macronucleus then increases in size and assumes the characteristic horseshoe shape.

Reorganization of the denticulate ring occurs in the macroconjugant shortly after fusion of the protoplasmic contents of the two conjugants. A new ring is formed outside the old in the same manner as in fission, but in this case the number of denticles in the new ring is the same as in the old.

While, as previously mentioned, the writer has observed conjugation in eight species, considerable numbers of conjugants have been available for study only in *T. symmetrica*, *T. californica*, and *T. discoidea*. However, it is evident that the process is essentially the same in all species studied. The greatest handicap to a study of the details of conjugation is the virtual impossibility of following the micronuclei throughout the process. During mitosis the micronuclei can be recognized without great difficulty, but at other times they are usually indistinguishable from the rounded remnants of the macronuclei which are scattered throughout the endoplasm. Consequently, there are many breaks in the sequence of events which can only be bridged by assumptions.

In general, conjugation in the species studied is similar to the process in *T. spheroidesi*, as described by Padnos and Nigrelli, but there are some important differences. These investigators emphasize the fact that in *T. spheroidesi* the conjugants are always unequal in size and their account of the entire process is based on this conception. On the other hand, Diller (1928) found that in the few conjugating pairs seen by him, the two conjugants were of the same size. The writer has found both conditions, sometimes even in the same species. In *T. discoidea* and *T. symmetrica* (figs. 182 and 184) the upper conjugant is usually smaller than the lower, but the difference in size is not great and occasionally the two conjugants may be practically equal in size. In *T. californica*, however, the conjugants are normally of the same size and no distinction can be drawn between macro- and micro-conjugants. It seems probable that where the conjugants differ in size, this difference is due to their relative age. This can best be seen in *T. discoidea*, since in this species the striations in the striated band stain more deeply than usual. In all conjugants of this species observed it was found that the smaller conjugant was younger than the larger conjugant (figs. 187 and 188). On the other hand in *T. californica* where the two conjugants are of the same size, the condition of the striated band in each conjugant indicated that they were approximately the same age.

As found by Padnos and Nigrelli, the conjugants in all species unite before there is any noticeable

change in the structure of either conjugant (figs. 182–184) and protoplasmic continuity soon becomes established between the two. The micronuclei begin to swell and soon leave their position near one arm of the macronucleus, moving to the center of the body just underneath the adoral surface where they divide mitotically. During the prophase the greatly enlarged micronuclei are characterized by a central rounded mass of chromatin surrounded by a large, clear area. Later the mitotic figure is formed within this space in the usual manner. The most striking aspect of mitosis is the extraordinary length of the spindle during late anaphase and telophase when it may become considerably longer than the diameter of the body. A similar condition has been described in other ciliates.

During division of the micronucleus, the macronucleus undergoes extensive changes. It becomes greatly elongated and attenuated with the formation of slender arm-like processes (figs. 186 and 189). Later the entire nucleus breaks up into small, rounded structures, each resembling a small nucleus (fig. 192). These may be uniformly granular or they may contain a rounded body in the center.

It has been impossible to follow the divisions of the micronucleus in the two conjugants, but there is no reason to doubt that Padnos and Nigrelli are correct in assuming that there are two divisions, one following immediately after the other. It is worth mentioning, however, that the nuclei in each conjugant are always in practically the same stage.

Fusion of a micronucleus from each conjugant to form the synkaryon is evidently followed by three divisions of the latter in quick succession, resulting in eight nuclei, seven of which form the macronuclear anlagen, while the other forms the functional micronucleus. At first it is impossible to distinguish these nuclei from the fragments of the original macronucleus since they are practically identical in appearance (fig. 192). At a little later stage, however, the macronuclear anlagen can be easily recognized by their larger size and finely granular contents (fig. 193). While these changes are taking place in the nuclei a new denticulate ring is formed to replace the old (figs. 190 and 191), but in this case the new ring has the same number of denticles. Following the development of the macronuclear anlagen and new denticulate ring, the exconjugant divides in the usual way except that only the micronucleus divides, while part of the macronuclear anlagen pass into each daughter cell along with fragments of the macronucleus. Figure 196 shows an individual with two macronuclear anlagen and figure 197 a later stage with one which is already developing into the macronucleus.

The writer has been unable to find any evidence that following division of the micronuclei in each conjugant the two fuse as described by Padnos and Nigrelli. On the contrary it is believed that a mutual exchange of micronuclei takes place between the two conjugants, although it is realized that the evidence is by no means conclusive. If this is the case, conjugation in *Trichodina* more nearly resembles that of *Paramecium* than of *Vorticella*, as held by Padnos and Nigrelli. In addition to the fact that no evidence has been found of the absorption of one conjugant by the other, strong support for the view that union of the conjugants is temporary has been found in *T. discoidea*. Two pairs in a late stage of conjugation were observed in which both conjugants showed a ring of overlapping plates in the striated band, which is the first indication of the formation of a new denticulate ring. Moreover, several juvenile exconjugants were found in which a new ring was being formed with the same number of denticles as the old. These individuals also contained macronuclear anlagen and rounded fragments of the macronucleus (figs. 194 and 195) as found in the larger exconjugants.

Diller (1928) has described in detail nuclear changes in a species of *Trichodina* from tadpoles which he believed to be endomixis. Padnos and Nigrelli point out that the endomictic stages described by Diller conform closely to the postconjugative stages in *T. spheroidesi* and conclude that he has misinterpreted postconjugation for endomixis. With this conclusion, the writer is in complete agreement. Stages similar to those described by Diller have been observed in all species which contained conjugating forms and are undoubtedly normal postconjugative stages. Diller states that there is little danger of confusing conjugation with endomixis in the *Trichodina* from tadpoles, since the macronuclear fragments instead of being spherical as in endomixis are rectangular, linear, or spindle-shaped. As a matter of fact, in all species observed by the writer the macronuclear fragments were elongated in early stages of conjugation, but later became rounded and similar to those described by Diller as characteristic of endomixis. In a later paper Diller (1936) admits the possibility that "hemixis and exconjugant stages" were lumped together in his account of endomixis in *Trichodina*.

Effects of Trichodinids on the Host

The trichodinids are among the most common protozoan parasites of fish and have been the cause of serious mortalities among trout and pond fishes at hatcheries. However, since they are frequently accompanied by other protozoan parasites such as *Chilodon*, *Costia*, and *Ichthyophthirius*, it is sometimes impossible to determine the relative importance of the trichodinids as pathogenic agents. Trichodinids may occur on the body, fins, and gills, although several species are confined to the latter. Two species have been described by Mueller (1932, 1938) from the urinary tract of fishes, but they should be relegated to his genus *Vauchomia* and are not considered here. Trichodinids can be seen moving about over the integument and gills by means of the membranelles in the ciliary girdle and when dislodged are propelled through the water by the same organelles. Individuals of some species, such as *T. bursiformis* and *T. bulbosa*, probably may remain anchored in one spot for some time.

Trichodiniasis, the disease caused by these parasites, is characterized by white irregular blotches on the head and dorsal surface of the body, especially near the base of the dorsal fin. The fins may also become badly frayed in heavily infected fish. This is accompanied by sluggishness and a partial or complete loss of appetite. When an infected fish is viewed in a bright light at the proper angle, a white translucent covering or film can be seen extending over the body which in places reaches a considerable thickness, forming the white blotches previously mentioned. This film is composed of epithelial cells in various stages of disintegration. The scales may also become loosened and in extreme cases the skin may show a reddish tinge due to congestion of the blood vessels. A similar hyperplasia of the epidermis may be caused by infection with other parasites and is evidently the result of a general irritation and not a specific reaction to this particular parasite.

It is interesting to find that the hyperplasia of the epithelium, which is basically a protective reaction on the part of the host, actually benefits the trichodinid parasites since they feed on the epithelial cells thus formed. In some species the epithelial cells appear to form the principal if not the only food of the parasites. Many instances of the ingestion of epithelial cells by *T. fultoni* (fig. 120) have been noticed and epithelial cells in various stages of digestion have been observed in the food vacuoles of several species. A similar hyperplasia, though not as pronounced, may occur on the gills and no doubt explains an interesting observation by Mueller (1937) on infected bass in the Myakka River near Sarasota, Florida. At the end of the dry season, the river consisted of a series of separate pools in which the fish were concentrated in large numbers. In such a pool a number of largemouth bass were taken with gills heavily infected with *Trichodina*. These fish appeared on the verge of suffocation and were unable to swim, so that they could be readily caught in the hand. Other bass in the same pool were active and healthy and when taken with a net, showed no *Trichodina*.

Padnos and Nigrelli (1928) noted the presence of red blood cells in food vacuoles of *T. spheroidesi* and concluded that these parasites were capable of considerable tissue destruction. They also found that in exceptionally heavy infestations, the gill epithelium was completely destroyed, leaving large denuded areas among the filaments. Such a condition resulted in the death of the host. According to Guberlet (1926) tench (*Tinca tinca* Linné) in aquaria which were heavily infected with *Cyclochaeta domergui* (*C. guberleti*, McLennan) showed in addition to the white film on the body hemorrhagic areas in the skin, and in many cases the skin sloughed off in large patches.

Fish are infected by direct transmission and there is no evidence that the parasites can spread by any other means. Richardson (1937) found that 12 hours after the introduction of an infected trout into a container with 2 clean fish, the latter were as heavily infected as the former. He also found that the length of time the parasite can live off the fish depends upon the temperature. When a freshly dead or dying trout is placed in a container, the parasites will escape slowly from the host and settle on the bottom of the dish. This process continues for several hours and the parasites may live for 2–3 hours after leaving the host. At room temperature (22°–25° C.) live *Trichodina* escaped from the dead host during a period of 8 to 10 hours and were still capable of infecting other trout at the end of this time. At lower temperatures the process was greatly prolonged. At 11° C. live trichodinids were present on the dead host up to 72 hours and at 4.5° C. they survived for 140 hours after the death of the host. All parasites died quickly on drying and experiments to produce a resistant form were unsuccessful.

The descriptions that follow include all species of *Trichodina* known to occur on freshwater fishes in this country. It is believed, however, that these are only a small fraction of the total number.

Trichodina discoidea, n. sp.

[Plate 3, figs. 27–30; plate 9, figs. 109–116]

This trichodinid apparently occurs on a considerable variety of hosts. It has been found on the gills of the bluegill sunfish (*Lepomis macrochirus*), the black crappie (*Pomoxis sparoides*) and the rock bass (*Ambloplites rupestris*) at Kearneysville, W. Va. It was also found on the gills of the channel catfish (*Ictalurus punctatus*) from the Mississippi River at Fairport, Iowa. In every instance it was associated with other species of *Trichodina* including *T. myakkae*, *T. symmetrica*, *T. fultoni*, and *T. bursiformis*. In most cases it was present in only relatively small numbers, but it was abundant on the gills of three bluegill sunfish from a hatchery pond at Kearneysville, W. Va. in April 1944.

Trichodina discoidea well exemplifies the characteristic features of the genus. The adoral surface is usually only slightly elevated and may be perfectly flat. Occasionally, however, the central part may form a rounded dome in striking contrast with the flattened margin of the body (fig. 115). The adoral spiral makes slightly more than one complete turn around the body and bears throughout two rows of long cilia. The margin of the body supporting the velum varies greatly, but is usually thicker than usual with a well-defined shallow groove which bears the membranelles of the ciliary girdle. A row of marginal cilia is present just above the membranelles. The adhesive disk is large and flattened with a diameter greater than that of the rest of the body. The denticulate ring may contain from 18 to 30 denticles, the usual number being 20 to 25. The hooks have the usual broad blade-shape, but this can be made out only in the adults (fig. 109). In juveniles the hooks appear much narrower (figs. 113 and 114). At all ages the outer edge of the hooks is less rounded than usual so that they appear to be truncated, a characteristic of this species. The rays are long, slender and sharply pointed. In the striated band there are 6 to 8 rods to each denticle. The border membrane (fig. 109) is wider and more distinct than in most species. The row of cilia above the membrane is well developed and easily distinguishable in sections. The diameter of the denticulate ring in adults varies from 19 to 29 μ and that of the striated band from 35 to 50 μ.

The macronucleus has the usual structure with the small, oval micronucleus located in a slight depression in the outer side of one arm. The contractile vacuole is well-defined, and can be seen to open to the exterior at the left of the mouth.

Trichodina discoidea is more variable than most species with respect to size and number of denticles. In fact, it was thought at first that two distinct species were present, but further studies showed that in other respects there was no appreciable difference between the large and small forms and that all intermediate stages could be found. As might be expected, the larger individuals usually had more denticles than the smaller. There is evidence of the presence of different strains or races in which the number of denticles is relatively constant. For example, denticle counts in 10 trichodinids selected at random from the gills of 3 sunfish from the same pond were as follows: fish A, 21, 22, 20, 20, 20, 22, 21, 22, 20, 20; fish B, 21, 22, 21, 21, 19, 21, 19, 21, 22, 22; fish C, 26, 23, 22, 22, 23, 23, 23, 26, 23, 24.

Conjugating pairs and exconjugants were common on the gills of bluegill sunfish examined in April 1944. Individuals in various stages of fission were also numerous. It is an interesting fact that in all species when conjugating forms are present, vegetative forms undergoing binary fission are also common. No conjugating or dividing stages were found on the rock bass and crappie. Only small numbers of this species were present and these averaged larger than those on the bluegills. Apparently trichodinids continue to grow after they mature and if for any reason fission is delayed, may become larger than usual. This would explain the presence of exceptionally large individuals which have been observed in several species.

Trichodina platyformis, n. sp.

[Plate 3, fig. 34; plate 9, figs. 117, 119, and 121]

Trichodina platyformis occurred on the gills of the pearl minnow (*Margariscus margarita*) and the dace (*Rhinichthys atronasus*) at Kearneysville, W. Va., during the spring of 1944. While a few specimens were found on most of the minnows examined, it was never abundant, and occurred even less frequently on the dace. Probably on account of its large size, it was more common on the gill arches than on the filaments and only very rarely was found between the lamellae.

This species is larger than most with a saucer-shaped body which is elevated into a low, rounded dome on the adoral side and shows little variation in form. The adoral spiral extends about one and one-fourth times around the body with two rows of

long cilia which, as usual, are motionless except near the mouth. Sometimes these cilia were folded back against the surface of the body and in that position were difficult to distinguish. The wrinkles around the margin of the adoral surface are usually prominent and 3 to 4 in number.

A row of marginal cilia is present. The adhesive disk is flat with the border membrane extending beyond the velum. The denticulate ring is well-developed and contains from 26 to 35 denticles, the usual number being 28 to 31. One exceptional individual was observed with only 20 denticles which were the usual shape and size. The broad, flat hook is so wide that the convex edge is nearly in contact with the concave side of the adjoining hook. The rays are long (10μ) and slender, sharply pointed at the end. The striated band has 10 rods to each denticle. The diameter of the denticulate ring is from 31 to 50μ and that of the striated band from 56 to 70 μ.

The macronucleus has the usual form with a comparatively large micronucleus near one arm. The latter contains an oval endosome with broadly rounded ends. The contractile vacuole is easily seen in the living organism and opens to the left of the mouth by a separate duct.

This species resembles *T. truttae* in many respects, but can be easily distinguished by its much smaller size. There are also fewer bars in the striated band.

Trichodina vallata, n. sp.

[Plate 3, fig. 32; plate 9, figs. 123 and 124; plate 10, fig. 126]

Some years ago fingerling channel catfish (*Ictalurus punctatus*) in a rearing pond at the Fishery Biological Station, Fairport, Iowa, became severely infected with *Costia necatrix*. An examination of these fish disclosed that, in addition to the flagellate, numerous specimens of an undescribed trichodinid was present on the body. That is the only time this species has been seen.

The adoral surface is moderately convex and presents no distinctive features with the exception of the adoral spiral which forms a circular ridge around the body (fig. 32). This ridge bears a narrow groove from which arise two rows of long cilia. Since the adoral spiral is so different from that of any other trichodinid, it provides a convenient means of distinguishing the species. The extent to which the adoral spiral is elevated varies, the two extremes being represented in figures 123 and 124. It makes about one and one-fourth turns around the body. The marginal cilia are well-defined.

The adhesive disk is very similar to that of *T. discoidea*. The average number of denticles, however, is less and the number is remarkably constant. A count of 25 specimens taken at random showed a range of 18 to 21 with the great majority having 19 or 20 denticles. There are 10 rods to each denticle in the striated band as compared with 6 to 8 in *T. discoidea*. The diameter of the denticulate ring ranges from 25 to 30μ, and that of the striated band from 38 to 48μ.

Trichodina fultoni, n. sp.

[Plate 5, figs. 46–48 and 54; plate 9, figs. 118, 120, 122, and 125; plate 10, fig. 127; plate 12, figs. 170–175]

This large species of *Trichodina* is common at the Fish and Wildlife Service hatchery, Kearneysville, W. Va. It has been found on several species of fish including the largemouth black bass (*Huro salmoides*), the smallmouth bass (*Micropterus dolomieu*) the bluegill sunfish (*Lepomis macrochirus*), the rock bass (*Ambloplitis rupestris*), the rainbow trout (*Salmo irideus*) and several species of minnows. It is possible that the occurrence of this trichodinid on such a variety of hosts was due to the crowded conditions characteristic of all hatcheries and that in nature its range is more restricted. It is ordinarily found on the body and fins, but may occur on the gills, especially in large fish. It is the most common species at the Kearneysville hatchery and has at times caused considerable mortality among pond fishes.

Trichodina fultoni is one of the largest of the trichodinids, being exceeded in this respect only by *T. truttae*. The adoral surface of the body may be flat or slightly convex. The adoral spiral makes an almost complete circuit of the body, but is not present in the space between the arms of the macronucleus. Along most of its length the cilia are very short and difficult to distinguish. Between the adoral spiral and the velum there are several concentric folds which are better developed than usual. The marginal cilia are also more distinct than in most species and in the living animal can be made out without difficulty when it is viewed from the adoral side. The number of denticles ranges from 25 to 30, the usual number being 27 to 29. The hooks are broad and well defined. The rays are short and curved in the same direction as the hooks (figs. 54 and 125). There are 12 to 14 bars in the

striated band to each denticle. In the adults the diameter of the denticulate ring ranges from 50 to 58μ, and that of the striated band from 75 to 90μ. The over-all diameter of the body in the living organisms is about 100μ.

The large horseshoe shaped macronucleus has the usual structure, but the micronucleus is very difficult to locate. In all other trichodinids studied the micronucleus could be identified without difficulty, but in the great majority of the specimens of *T. fultoni* it has been impossible to distinguish this structure with certainty. It is of the usual vesicular type with a large endosome and may lie underneath the macronucleus where it is not readily seen. To add to the difficulty, the endoplasm contains numerous food vacuoles filled with fragments of tissue cells which stain deeply. The large contractile vacuole is located in the center of the body just above the adhesive disk and is provided with a small duct which opens to the exterior through a narrow slit slightly above and to the left of the mouth (fig. 118).

Trichodina fultoni is believed to be identical with the form described by Fulton (1923) from the gills of *Necturus*. Fulton's description of the parasite is incomplete and his only figures are photomicrographs which fail to bring out some of the essential details, but in size and general appearance there is a close resemblance between the two organisms. Fulton transferred specimens to the body of Hydra and "found that they crawled on the surface of the polyp quite as in the forms normally there." On this entirely inconclusive evidence he identified his form as *T. pediculus*. Furthermore, it is evident that several species have been included in *T. pediculus* by earlier writers, none of which appear to be identical with the present form. Since Mueller (1937) has discussed in some detail the questionable basis for Fulton's identification it is unnecessary to go into the matter further. Nevertheless, Mueller followed Fulton, though with some misgivings, and identified a trichodinid which he found on the gills of the largemouth black bass from the Myakka River near Sarasota, Florida, as *T. pediculus*. Mueller's description of the parasite is more complete and while his form differs in some details from that found at Kearneysville, it is not believed that the differences are sufficient to justify considering them to be specifically distinct. The size is approximately the same, but the number of denticles averaged slightly less (23 to 26), although the range overlaps. Also in Mueller's figures the rays are somewhat longer and less curved than in the writer's material. Finally, Mueller found about 9 bars in the striated band to each denticle while the Kearneysville form has 12 to 14 bars. In other respects the two forms appear to agree.

Trichodina truttae Mueller

[Plate 5, fig. 53; plate 10, figs. 129 and 130]

Specimens of a trichodinid preserved in formalin were received from G. C. Webb, Philomath, Oregon. These parasites occurred on the body of fingerling cutthroat trout (*Salmo clarkii*) at the Alsea hatchery of the Oregon State Game Commission. They agree very closely with a trichodinid described by Mueller (1937) from the gills of cutthroat from Oregon.

The body of the parasite is flattened and saucer-shaped. The denticulate ring contains from 28 to 31 denticles while Mueller found from 28 to 30 in his material. The striated band has 20 rods to each denticle. The denticles bear a flattened blade-like hook which is even broader than usual. Mueller, on the contrary, describes the hook as much narrower, but it is believed the discrepancy can be explained by the fact that he had only stained whole mounts for study. The blade part of the hook is thinner than usual and even in formalin material is so transparent that it is easily overlooked. The rays are long and slender as described by Mueller. He emphasizes the fact that the hook and ray of each denticle are not opposite each other as in other species, but that the hook is ahead of the ray. While this is frequently the case, there is considerable variation in this respect and both conditions may occur in the same individual. The adoral surface is only slightly elevated and the adoral spiral makes slightly more than one complete circuit of the body. The cilia are short throughout, except in the immediate vicinity of the mouth.

This species is notable for its size. In full-grown individuals the denticulate ring has a diameter of 75 to 85 μ, and the striated band a diameter of 110 to 125 μ. The overall diameter of the body, exclusive of the ciliary girdle is about 130 to 140 μ in preserved specimens.

Trichodina symmetrica, n. sp.

[Plate 5, figs. 49–52; plate 10, figs. 134–136, 138, and 139]

Trichodina symmetrica was first found on the gills of the channel catfish (*Ictalurus punctatus*) from the

Mississippi River at Fairport, Iowa. Several fish taken during July and August were infected. Later it was found on the gills of the pearl minnow (*Margariscus margarita*) and the dace (*Rhinichthys atronasus*) collected during the spring and early summer at Kearneysville, W. Va. The parasite was not abundant but a large percentage of the fish examined were infected.

This species shows less variation in shape than most trichodinids. The adoral surface forms a low, rounded dome with the mouth located somewhat higher on the surface than usual. The adoral spiral extends about two-thirds of the distance around the body. The cilia are relatively long and vary but little in length throughout the course of the spiral which ends abruptly instead of fading out gradually. The velum is thick, frequently poorly defined, and without wrinkles on the adoral surface. There are from 21 to 28 denticles in the denticulate ring, the usual number being from 24 to 26. The hooks are spatulate and rounded at the end, the rays are slender and frequently difficult to distinguish. The striated band contains about 5 rods to each denticle and in suitably stained specimens it is evident that there is a striation or bar for each membranelle in the ciliary girdle. The row of cilia on the adoral side of the border membrane is better developed than usual and extends a short distance beyond the edge of the membrane. The diameter of the denticulate ring ranges from 13μ to 22μ and that of the striated band from 24μ to 35μ.

The macronucleus has the usual horseshoe shape, but shows a tendency to assume unusual forms, such as an outgrowth of one arm which, in one instance, was connected with the opposite arm above the mouth. The micronucleus is spindle-shaped, even in the resting condition, and frequently lies in a depression in one arm of the macronucleus.

During binary fission the velum disappears and the margin of the body becomes noticeably thicker, so much so in fact that sometimes the body has the same thickness throughout. In such individuals the adoral spiral forms a border for the flattened adoral surface. Conjugating individuals were common both at Fairport and at Kearneysville.

Trichodina californica, n. sp.

[Plate 4, figs. 39, 41, 43, and 45; plate 10, figs. 131–133, 137, and 140]

During the fall of 1943, adult chinook salmon (*Oncorhynchus tschawytscha*) from the Sacramento River, Calif., showed a heavy infection of the gills with this trichodinid. The fish had been held for several weeks in ponds at the Coleman hatchery on Battle Creek. Only preserved material has been available for study.

Trichodina californica is characterized by an unusual plasticity resulting in marked changes in form so that the general appearance of the organism may vary greatly. The adoral surface of the body is raised into a rounded dome which is usually unsymmetrical, the greatest bulk being at one side. Occasionally the adoral surface is flat instead of convex and all intermediate stages can be found. In such individuals the body may project some distance beyond the adhesive disk on all sides, as in figure 41. More often, however, the bulk of the body is on one side (fig. 43), so that in sections it appears very unsymmetrical. The adoral spiral makes a complete circuit of the body and may, as in other species, be located entirely on the adoral surface, but usually during part of its course it occupies a groove in the margin (fig. 41). The cilia are relatively short and inconspicuous. Concentric wrinkles may be present on both sides of the adoral spiral, but there is great variation in their number and shape. The denticulate ring contains from 25 to 32 denticles, the usual number being 26 to 28. The hooks are wide and blade-shaped, the rays straight and pointed at the end. The striated band contains 8 to 10 bars to each denticle. The denticulate ring has a diameter of 25 to 33μ, and the striated band a diameter of 38 to 50μ.

The macronucleus has the usual horseshoe shape and is filled with fine chromatic granules among which are numerous rounded nucleoli. The ovoid, vesicular micronucleus is located at the side or underneath one arm of the macronucleus. Food vacuoles are numerous in the endoplasm.

Conjugating forms and individuals in various stages of binary fission were common, but owing to poor fixation were not as valuable for study as similar stages in other species.

A remarkable condition, which has not been found in other species, was observed in a small percentage of the parasites. These individuals contained a deposit of amorphous material in the endoplasm which was usually first noticeable near the adoral surface. Eventually, the entire organism became filled with this material (figs. 133 and 137) and then appeared to be enclosed in an opaque covering which was a glistening white by reflected light. The composition of this material is not known, but it is ap-

parently an organic substance since it is not affected by hydrochloric acid. It was most noticeable in specimens preserved in formalin, but was not affected when they were embedded and sectioned. In sections of parasites fixed in formol-mercuric-acetic fluid the deposit had largely disappeared. No explanation could be found for this condition.

Trichodina californica can be easily recognized by the small size of the adhesive disk as compared with the rest of the body. In this respect it most closely resembles *T. tumefaciens*, but is considerably larger and the denticulate ring is quite different in the two species.

Trichodina tumefaciens, n. sp.

[Plate 4, figs. 36 and 37; plate 10, figs. 141 and 142; plate 11, figs. 143–148]

The gills of sculpins (*Cottus bairdii*) taken from a small brook near Kearneysville, W. Va., were infected with a trichodinid which may be restricted to this host, since it was not found on other fishes collected at the same time. It was present on practically every sculpin examined and in many instances was abundant.

Trichodina tumefaciens, like *T. californica*, is characterized by the relatively large size of the adoral part of the body, which is usually strongly convex, but has an unusual capacity to change its shape. It shows the same tendency as *T. californica* for the bulk of the adoral dome to be located at one side instead of over the center of the adhesive disk. The cilia of the adoral spiral, which extends about one and one-fourth times around the body, are exceptionally long. Outside the adoral spiral are several concentric wrinkles which are more prominent than usual. When the adhesive disk is curved downwards so as to form a cup-shaped structure these wrinkles are smoothed out. There is a well-defined row of marginal cilia. The denticulate ring contains from 19 to 26 denticles, the usual number being 21 to 25. The striated band has about 7 bars to each denticle.

This species is notable for the marked change that occurs in the denticulate ring during the life of the individual. No doubt similar changes occur in all trichodinids, but in *T. tumefaciens* they are more noticeable than in most species. In fact, the difference between juveniles and adults is so great that they were at first thought to be different species. In the juveniles the hooks are narrow, and the rays slender and pointed (figs. 143 and 144). Figure 145 represents an intermediate stage in which both hooks and rays are larger and wider. Finally, in the adults (fig. 146) the hooks have the usual blade-like shape while the rays are broad and rounded at the end.

The diameter of the denticulate ring varies from 18 to 23μ and that of the striated band from 29 to 38μ.

The macronucleus and micronucleus have the usual structure and there is nothing distinctive about either. The cytopharynx forms a relatively large tortuous tube nearly as long as the diameter of the adoral dome. The contractile vacuole is more conspicuous than in most species with a separate duct to the exterior which is easily seen. Various stages in conjugation were observed but they were not common.

Trichodina bulbosa, n. sp.

[Plate 3, figs. 31, 33, and 35; plate 11, figs. 149–157]

This interesting trichodinid was found on the gills of the pearl minnow (*Margariscus margarita*) at Kearneysville, W. Va., during the spring and early summer of 1944. These fish were collected from the same brook as the sculpins infected with *T. tumefaciens*, but only the pearl minnows carried the present species which was found on nearly every fish examined.

Trichodina bulbosa is quite different from most species of *Trichodina*. It is shaped like a turban rather than the usual saucer shape. The adoral surface may be rounded or cone-shaped and the adhesive disk is strongly curved to form a cup-like structure. The adoral spiral extends about three-fourths of the distance around the body, but follows an unusual course. From the mouth it extends upwards along one side of the body until it reaches the crest of the dome and then drops down and terminates just above the denticulate ring. Throughout its course the cilia are exceptionally long and usually erect, but may be bent toward the center so as to lie in contact with the adoral surface. Sometimes there may be one or more wrinkles near the base of the velum, but they are never a prominent feature. There are 19 to 24 denticles in the denticulate ring, the usual number being 21 or 22. The hooks are exceptionally long and paddle-shaped with their greatest width near the outer end. The rays are slender and pointed. The striated band is wider than usual with 5 to 6 bars to each denticle. The diameter of the denticulate ring when flattened is 10μ to 12μ, and that of the striated band 22μ to 26μ.

The macronucleus has the usual horseshoe shape

and lies just above the denticulate ring with the vesicular micronucleus underneath one arm (fig. 31).

The parasites cling to the gills in a very characteristic manner by means of the adhesive disk which encloses the edge of a lamella. Considerable pressure is evidently exerted by the edge of the disk, since the epithelial cells may be forced to one side as in figure 154 so that in sections the margin of the lamella appears to be separated from the main part by a narrow neck. This, however, is not so marked as with *T. bursiformis*.

Conjugating individuals were observed in several instances (fig. 185), the process being essentially the same as in other species. Both conjugants were of approximately the same size, and the upper clung so closely to the lower as to narrowly constrict the body of the latter.

Trichodina bursiformis, n. sp.

[Plate 4, figs. 38, 40, 42, and 44; plate 11, figs. 158–165]

This interesting species has been found only on the gills of the rock bass (*Ambloplites rupestris*) from Opequon Creek near Kearneysville, W. Va. Two fish with a severe infection with this trichodinid were taken in March 1943. In both fish a much smaller number of *Trichodina discoidea* were also present on the gills.

Trichodina bursiformis is very different from other known trichodinids and most nearly resembles *T. bulbosa*. In fact, this species shows an extreme development of the features which differentiate the latter from other forms. The structure of this bizarre organism is difficult to describe, especially since the body is very plastic and the shape very variable. When free-swimming, the animal resembles an old-fashioned sunbonnet with the elevated adoral surface forming the crown. The adhesive disk, instead of being expanded in the usual manner, is compressed, bringing the border of the opposite sides close together with a long, narrow opening between (figs. 42 and 162). This apparently always takes place in the plane which passes through the mouth. The adoral surface is also compressed in the same plane so that instead of the usual dome it forms a ridge extending from the mouth to the opposite side of the disk. This ridge may vary greatly in shape; sometimes it is low and comparatively broad, sometimes high and narrow. A band of long cilia, the adoral spiral, extends along one side of the ridge and around each end. At one end it enters the mouth, at the other end it terminates in a tuft of longer cilia which is very conspicuous. As usual, the cilia in the adoral spiral show no movement, except near the mouth, and are frequently folded inwards over the adoral surface instead of standing erect. As in *T. bulbosa*, the adoral spiral extends upward from the mouth along the ridge and then drops down to the level of the denticulate ring.

In cross sections of the organism (figs. 40, 160, 161, and 164) the adhesive disk appears as long arm-like structures projecting from each side of the body. As shown in the figures, one arm is usually somewhat shorter than the other. The velum is well-defined and in sections appears as a thick lobe projecting over the base of the ciliary girdle. At the base of the velum there are several narrow, concentric wrinkles. The denticulate ring is well-developed, but evidently has even greater flexibility than usual. The hooks are spatulate, very similar to those of *T. bulbosa*. The rays are long and slender, but somewhat enlarged at the base. The ring is composed of 24 to 27 denticles with a diameter of 14 to 18μ. The striated band is about 25 to 35μ in diameter with 5 bars to each denticle. The macronucleus has the usual horseshoe shape, but one arm is frequently longer than the other. The vesicular micronucleus is ovoid and may lie between the arms of the macronucleus or at one side.

When attached to the gills the adhesive disk serves as a clasping organ which grasps the edge of the lamella with such force as to squeeze the epithelial cells out of position (figs. 160, 161, and 164). This method of attachment is more highly developed than in *T. bulbosa* and apparently the parasites may remain in one position for some time. However, when the gills are removed from the fish, they quickly become detached and swim about rapidly with the narrow opening of the adhesive disk foremost.

As already pointed out, *T. bursiformis* resembles *T. bulbosa* in many respects, but can easily be distinguished by its larger size and compressed body. The adoral spiral is also more prominent with longer cilia.

Trichodina myakkae Mueller

[Plate 5, figs. 55–58; plate 11, figs. 166–169]

This trichodinid was found by Mueller (1937) on the gills of the largemouth black bass from the Myakka River near Sarasota, Fla. Later (Mueller 1938), he reported its occurrence on carp and suckers from Chautauqua Lake, N. Y. The writer first

found *T. myakkae* on the gills of the smallmouth buffalo (*Ictiobus bubalus*) and the carp sucker (*Carpiodes carpio*) from the Mississippi River at Fairport, Iowa. During November and December 1944 it was present in considerable numbers on the gills of brook trout (*Salvelinus fontinalis*) in a hatchery pond at Kearneysville, W. Va. Evidently this species can live on a wide variety of hosts.

The organisms observed by the author agree in all essential respects with Mueller's description. The adoral surface is usually strongly convex, but may be much lower in some individuals than in others. The adoral spiral extends from one-half to two-thirds the distance around the body. The cilia are exceptionally long and near the mouth may equal the membranelles of the ciliary girdle in length. The groove bearing the ciliary girdle is shallow and poorly developed. The denticulate ring has a very characteristic structure which serves to distinguish this species from other known forms at a glance. The hooks are straight and narrow and the rays are entirely lacking. The striated band has 4 to 5 bars to each denticle and when properly stained can be plainly seen to have a bar for each membranelle (fig. 58). The number of denticles may vary from 17 to 24. In specimens from Fairport the number was somewhat less than in those from Kearneysville. In the former the usual number was 19 to 20, while in the latter it was 20 to 23. Mueller found 18 to 22 denticles in his specimens. The diameter of the denticulate ring in adults was remarkably constant, ranging from 11 to 12μ, while the diameter of the striated band varied from 21 to 25μ.

The macronucleus has the usual granular structure and horseshoe shape. The micronucleus is greatly elongated (fig. 57), much more so than in other species. It is usually located in a depression in an arm of the macronucleus and may be so closely attached as to be difficult to distinguish. Food vacuoles containing bacteria are usually present and it is probable that they form the principal food of this species. This is to be expected, since *T. myakkae* is too small to ingest epithelial cells.

Family **Scyphidiidae** Kahl

Scyphidia macropodia, n. sp.

(Plate 6, figs. 67–72; plate 13, figs. 198–208; plate 14, figs. 209, 217, and 218)

A number of fingerling bullheads (*Ameiurus nebulosus*) which were confined in a concrete tank at the Fish and Wildlife Service Station, Kearneysville, W. Va., during August 1943, became heavily infected with an undescribed scyphidian for which the name *Scyphidia macropodia* is proposed. The parasite was abundant on the gills and body of the fish and caused considerable mortality. A few scyphidians were found on the gills of fingerling bluegills (*Lepomis macrochirus*) in an adjoining tank, but it seems probable that the infection in this case was accidental. Several specimens of the same parasite have been found on the gills of the channel catfish (*Ictalurus punctatus*) from the Mississippi River at Fairport, Iowa.

Morphology

The body of *Scyphidia macropodia* is cylindrical with approximately the same diameter throughout, but occasionally may be somewhat constricted near the base. It is attached to the epithelium by means of a holdfast organ, the scopula, which in this species is exceptionally large. The scopula is a very flexible expansion of the aboral or posterior end of the animal and conforms to the surface contours of the epithelium. The peristome at the adoral or anterior end has a slightly greater diameter than the body proper. About one-third of the distance between the scopula and the peristome there is a membranelle which extends around the body like a collar. In the living organism it is difficult to distinguish the cilia in the membranelle, but sometimes they are separated along the outer margin. When viewed from the adoral surface the membranelle shows a slow, undulatory movement. On both sides of the central membranelle the pellicle is marked by parallel transverse striations extending around the body. There are about 16 of these striations between the peristome and the membranelle.

The border of the peristome consists of a thick, lip-like structure which by constriction closes over the disk when the animal retracts (figs. 70 and 199). Just within the border is the adoral groove bearing two parallel rows of cilia. As found by Noland and Finley (1931) in Vorticella, the cilia are united at the proximal end to form a "semi-membranelle," but are usually separated at the tips so that the membranelle has a ragged edge. The cilia in the outer row, however, sometimes appear to be united throughout their length. The cilia in the inner row are much longer and thicker than those in the outer. The two rows of cilia form the adoral spiral which, when viewed from above (fig. 67), can be seen to follow a spiral course anticlockwise around the peristomial

disk. The course of the adoral spiral is the same as in *Trichodina* and makes about one and one-fourth turns around the disk. At one side the adoral spiral leads into the vestibule, and as they enter the membranelles diverge from each other for a short distance, but soon come together again to follow a spiral course around the vestibule. Since the adoral spiral makes more than a complete circuit of the peristomal disk, four rows of cilia are present for a short distance near the opening into the vestibule (fig. 71). Within the adoral spiral the surface of the peristome is smooth and convex.

The contractile vacuole is located just beneath the central convex surface of the peristome and opens at one side into the vestibule. The most conspicuous structure within the body is the large, deeply stained macronucleus which is very similar to that of *S. tholiformis* (Surber 1943). The macronucleus is a long, sausage-shaped structure with two arms extending the length of the body and connected by an open loop around the vestibule. The ends of the nucleus lie just above the scopula in a tangled mass, the exact arrangement depending on the amount of retraction. There is, however, no branch or "prong" from an arm of the nucleus as in *S. tholiformis*. The macronucleus is uniformly and finely granular with practically the same structure throughout. The micronucleus is located among the tangled ends of the macronucleus and is composed of a rounded mass of deeply staining granules embedded in a homogeneous matrix which is separated from the nuclear membrane by a clear halo. Numerous food vacuoles are usually present in the finely granular endoplasm.

The living organism when fully extended is about 35 to 45μ in length with a width of 20 to 25μ.

In addition to the attached stage described above, the organism may change into a free-swimming or telotroch stage (figs. 201 and 202) as described by Surber (1943) for *S. tholiformis*. The transformation takes place very rapidly when the parasites are removed to a slide, but occurs in only a small percentage of the organisms. The change is accomplished by an extreme shortening of the body so that it becomes disk-shaped and has a striking superficial resemblance to a trichodinid. The scopula is retracted to form the lower surface of the telotroch, while the convex upper surface is formed by the constricted border of the peristome which covers the peristomal disk, except for a small opening in the center. At the same time the cilia in the central membranelle become free, increase in length, and form the locomotive organ in the same manner as the ciliary girdle of trichodinids.

Reproduction

Like other scyphidians, *S. macropodia* reproduces asexually by binary fission. In this process (fig. 205) the organism divides lengthwise, the micronucleus dividing mitotically, followed by amitotic division of the macronucleus, which is first greatly shortened and then divides into two equal parts.

Although individuals in various stages of conjugation were not uncommon, it has been impossible to follow the entire process in detail. However, it appears to agree in most respects with conjugation in *Vorticella microstoma* as described by Finley (1943). The small free-swimming microconjugants are apparently formed by budding (fig. 218) from an ordinary individual.[4] The newly formed microconjugant is surrounded by a band of cilia and contains a U-shaped macronucleus and a single micronucleus. The microconjugant becomes attached to the macroconjugant near the peristome (figs. 70 and 217), but does not unite with it immediately. The micronucleus then forms eight nuclei of equal size by three rapidly recurring divisions. At the same time, the micronucleus in the macroconjugant divides twice to form four nuclei of equal size. During these divisions of the micronuclei the macronuclei of both conjugants remain unchanged.

The next stage in the process has not been followed but from analogy with other vorticellids we may assume that the eight micronuclei pass from the microconjugant into the macroconjugant. One of these becomes a pronucleus and unites with the pronucleus of the macrogamete to form the synkaryon. The remaining seven micronuclei of the microconjugant and three micronuclei of the macroconjugant then degenerate and take no further part in the process. During formation of the synkaryon the macronuclei of both conjugants break down into rounded structures similar to those formed in *Trichodina*. The synkaryon then divides twice to form four nuclei, three of which increase in size to form macronuclear anlagen while the fourth becomes the functional micronucleus (figs. 203, 204, 207, and 208). This does not agree with the findings of Finley and other investigators of conjugation in the peritrichous

[4] Penard (1922) found that the microconjugants in *Glossatella tintinnabulum* are formed by two rapidly recurring divisions resulting in the formation of four small individuals. A similar process has been observed in *S. macropodia*, but, as will be explained later, is believed to follow conjugation rather than precede it.

ciliates who have found that the postconjugants contain eight nuclei, seven of which develop into macronuclear anlagen as in *Trichodina*. The only exception is Enriques (1907) who found that in *Opercularia* only four nuclei were present in the post conjugant, three of which became macronuclear anlagen. Enriques gave as an illustration one with seven macronuclear anlagen and one micronucleus, which he believed to be exceptional, but Finley (1943) argues with some justification that this was probably a normal stage rather than an exception.

Postconjugants in *S. macropodia*, containing three macronuclear anlagen and one micronucleus were quite common, but although a special search was made, no individuals containing more than four nuclei could be found. Although the Feulgen stain was not used there was no difficulty in distinguishing the nuclei from the fragments of the degenerating macronuclei which were the only other structures taking the nuclear stain. Various stages in the development of the macronuclear anlagen were observed, but there were never more than three in any individual. They are spherical at first, finely granular and stain less deeply than the rounded remnants of the macronuclei. As the macronuclear anlagen increase in size, they become elongate and eventually U-shaped.

The postconjugant then divides by two rapidly recurring divisions into four individuals which are much smaller than usual and have a different appearance (figs. 68 and 206), due to the peristomal disk being entirely enclosed by the border. Figure 68 is a section of one of the daughter cells formed by the first division of the postconjugant. This individual contained a U-shaped macronucleus and a micronucleus in the anaphase preparatory to the second division. In the next section there was a similar individual with a dividing micronucleus, but with two U-shaped macronuclei. When these two individuals divide it is believed that in the one figured both the micro- and macronuclei divide, while in the other only the micronucleus would divide, one of the two macronuclei passing into each daughter cell. This would result in the formation of four individuals in a group as in figure 209. In support of this explanation of the formation of the group is the obvious fact that in the two individuals above and at the left the macronuclei are longer than in the other two. The former are believed to be the daughter cells of an individual with two macronuclei, while the latter were formed from an individual with one macronucleus which divided along with the cell. Although, as previously pointed out, Penard (1922) thought these small individuals became microconjugants, it is believed that the explanation given above is more in accord with the evidence.

Some attention was given to conjugation in *S. tholiformis* which appears to be essentially the same as in *S. macropodia*. The macronuclei, however, break down before the conjugants unite and consequently it is very difficult to follow the divisions of the micronuclei. Only a few postconjugants were found, but no more than three macronuclear anlagen could be distinguished in any individual.

Class SUCTORIA Clarapede and Lachmann

Trichophyra ictaluri, n. sp.

[Plate 6, fig. 73; plate 14, figs. 214, 222, and 223]

This suctorian was found on the gills of channel catfish from the Mississippi River at Fairport, Iowa. It was present on several fish out of a small number examined and although not abundant in any instance, is evidently not uncommon. This species was figured and described very briefly in a previous publication (Davis 1942). Since that time additional material has become available which makes a more complete description of the parasite possible. This description, however, is based entirely on preserved material.

In sections the parasites appear somewhat elongated with one side in close contact with the surface of the gill. The tentacles are arranged in bundles or fascicles and there is usually a fascicle at each end of the body. It was thought at first that two fascicles of tentacles was characteristic of this species, but an examination of unsectioned gills preserved in formalin disclosed that there may be from one to four fascicles of tentacles (fig. 214). The number appears to depend on the age of the parasite, small—and presumably young—individuals having only one bundle of tentacles. Individuals intermediate in size may have two fascicles, while full-grown suctorians may have four distinct fascicles of tentacles

evenly spaced around the body. No more than four have been observed in any individual. The tentacles are usually borne on smooth, rounded elevations, but sometimes the surface to which they are attached is quite irregular. The tentacles are somewhat enlarged at the free end and at the proximal end can be traced for some distance into the body where those of each fascicle converge toward a common point. It was impossible to determine their number, but there may be at least 10 to 12 tentacles in each fascicle. The body is covered by a thin, dense layer of ectoplasm, but there is apparently no distinct pellicle. The side of the body in contact with the epithelium may be convex or flattened and is closely attached to the lamella. Frequently the epithelial cells have been destroyed or pushed aside so that the parasite may be in direct contact with the capillary network (figs. 73 and 223).

The endoplasm is coarsely granular and ordinarily contains a number of rounded metaplastic bodies. In some instances these bodies were so abundant as to obscure all other structures. The macronucleus is large and may be rounded or sausage-shaped. It is filled with spherules of equal size which stain intensely with chromatic stains. In addition, there are usually one or more rounded bodies several times the size of the spherules which also stain deeply. No membrane could be distinguished around the macronucleus. The micronucleus is vesicular with a rounded endosome composed of chromatin granules in a nonstaining matrix which is separated by a clear area from the nuclear membrane.

The organisms vary greatly in size. The largest individual observed in formalin material with 4 fascicles of tentacles was 50 by 65μ. In sections the longest diameter was usually about 35–40μ and the thickness 15–20μ.

The parasite multiplies by endogenous budding. Several individuals were observed with buds nearly ready to emerge.

The only suctorian previously described from fish is *Trichphrya micropteri* (Davis 1942) from the gills of the smallmouth black bass. This species has only one bundle of tentacles so there is no possibility of confusing the two forms. There is no doubt that many other suctorians occur on the gills of fishes. The writer has specimens of several species, but the material is too fragmentary to permit a detailed description.

Order MYXOSPORIDIA Butschli

The Myxosporidia form a large and well-known group of Protozoa which are typically fish parasites, although a few species occur in amphibians and reptiles. It is, therefore, to be expected that any extensive study of protozoan parasites would disclose many members of this group. They are especially common on the gills of freshwater fishes and although many species have been observed, only two which are of more than ordinary interest, are considered here.

Family **Chloromyxidae** Thelohan

Chloromyxum externum, n. sp.

[Plate 7, Figs. 74–80, 82, and 83; Plate 14, Figs. 215, 216, 219–221, and 224]

Myxosporidians are typical endoparasites, being found in the tissues and cavities of the body, and their structure and life cycle are especially suited to this mode of life. It is, therefore, of considerable interest to find a myxosporidian which, while exhibiting the typical structure of the group, is a true ectoparasite. This species, for which the name *Chloromyxum externum* is proposed, lives on the surface of the gills and so far has been found only on the pearl minnow (*Margariscus margarita*) and the black-nosed dace (*Rhinichthys atronasus*). Infected fish of both species were collected from the same brook near Kearneysville, W. Va., during March, April, and May, 1944. The parasites are small and easily overlooked unless present in considerable numbers.

The trophozoites are very similar to those of many other species of *Chloromyxum*. They are colorless with a clear, hyaline layer of ectoplasm surrounding a finely granular endoplasm. The latter is faintly vacuolated and contains numerous small, refringent, fat globules (fig. 74). The trophozoites move slowly by means of a short conical pseudopodium formed of ectoplasm. In fixed material the ectoplasm is more distinctly reticulated than the endoplasm.

The nuclei cannot be seen in the living trophozoite, but after fixation and staining, two types of nuclei

can be distinguished without difficulty. The more numerous generative nuclei are surrounded by a dense layer of cytoplasm to form the generative cells (fig. 79). These cells are clearly set off from the undifferentiated endoplasm by the coarsely granular cytoplasm which takes the hematoxylin stain. Each nucleus contains a large, centrally located nucleolus or plasmosome which is surrounded by a clear area. There is no chromatic network, the chromatin, as is frequently the case in the Myxosporidia, being limited to a layer of fine granules attached to the nuclear membrane. The generative cells vary in size and are rounded to irregular in shape. Occasionally a generative cell may contain two nuclei, but usually each cell is distinct with only one nucleus until the spores start to develop. The vegetative nuclei can be easily recognized by the fact that they are not surrounded by a differentiated layer of cytoplasm. Otherwise, their structure is essentially the same as that of the generative nuclei except that they may be slightly smaller.

Naturally, the trophozoites show considerable variation in size. The dimensions of several large trophozoites selected at random in sections and smears were as follows: 14 by 32μ; 15 by 28μ; 16 by 19μ; 14 by 24μ; 15 by 20μ; 17 by 19μ; 16 by 27μ. Rounded trophozoites were 15 to 17μ in diameter.

The spore (fig. 80) is approximately spherical to ovoid with four polar capsules of approximately the same size in which the coiled filaments can be seen indistinctly. Each valve bears about six concentric ridges which are parallel with the sutural ridge. The fresh spore is about 8μ in diameter, but in sections they show considerable shrinkage, the diameter being only about 6μ.

REPRODUCTION

Sporulation is essentially the same as in other Myxosporidia. The generative cells become aggregated in groups of eight cells to form a sporoblast which develops into the mature spore in the usual manner. No pansporoblasts are formed and each sporoblast becomes a spore independent of other sporoblasts. Furthermore, it appears that, in most cases at least, only one spore matures at a time, although two or three spores in different stages of development may be present in the same trophozoite (fig. 77). How many spores may be produced by a trophozoite is not known, but it is evident that the species must be considered polysporous, even though no trophozoite has been found with more than two well-developed spores.

Although numbers of infected fish were collected during March, April, and May, sporulating trophozoites were found in only one instance. A black-nosed dace, collected on April 10, was heavily infected with vegetative and sporulating trophozoites. No evidence of sporulation could be found among the parasites of several pearl minnows collected at the same time.

It seems probable that, in addition to the production of spores, the trophozoites multiply by plasmotomy. This is a common method of reproduction among the Myxosporidia and while it has not been observed in *C. externum*, there is indirect evidence that it does occur. Naturally, plasmotomy is difficult to demonstrate under the best of circumstances, but with trophozoites living on the surface of the gills, the possibility of observing it is slight indeed. The best evidence that such a process must occur is furnished by the distribution of the trophozoites on the gills. Instead of being evenly distributed, they are always much more abundant on some gills than on others in the same fish and they are also more numerous on certain parts of the same gill. A few adjoining filaments, for instance, may have large numbers of trophozoites, while the rest of the gill is almost free from them. This cannot be due to differences in the structure or location of the filaments, since the heaviest infection may be found on almost any part of the gill.

Nothing is known regarding the means by which the parasites are transmitted from one fish to another. From analogy with other species of Myxosporidia, it must be assumed that the spores after dropping from the gills are ingested accidentally by other minnows and germinate in the stomach or intestine. The ameboid sporoplasm then enters a blood vessel and is carried to the gills. In fresh-water fishes the gills are among the organs most commonly infected by Myxosporidia. Most of the gill parasites are so-called histozoic forms which form cysts on the gill tissues, but, nevertheless, reach the gills by means of the circulatory system (Davis 1923, p. 431). Having reached the gills, it is assumed that the young trophozoites of *C. externum* leave the capilliaries and make their way through the epithelium to the surface. Although sections of infected gills have been searched carefully, trophozoites which were entirely surrounded by epithelial cells have been found in only one instance. In this case a group of several small trophozoites were located in the stratified epithelium lying between the lamellae. The appearance of the trophozoites in close contact

with each other suggests that they may have been formed by division of a single individual. Of course, the possibility is not ruled out that the spores may germinate on the gills after having become entangled in the mucus, but there is certainly no evidence that this ever occurs.

Relation of Parasite to the Host

As already pointed out, this species is of exceptional interest since it is the only known ectoparasite in the entire group of the Myxosporidia. The trophozoites are found attached to the surface of the epithelium or in the mucous coating surrounding the gills. In some instances they may be attached to the epithelium simply by a pseudopodium (fig. 78), but usually the entire organism is in close contact with the epithelial cells. Frequently the trophozoite lies in a saucer-shaped depression in the epithelium which appears to have been formed by lysis of the epithelial cells (figs. 83 and 215). Sometimes the cells have been entirely destroyed so that the trophozoite is in direct contact with the capillary network of the lamella (figs. 82 and 220). The trophozoites may fit so closely into the space formerly occupied by tissue cells as to appear at first glance to be an integral part of the epithelium.

In severe infections large numbers of trophozoites are found in the mucus which forms a protective coating over the gills. In such cases the secretion of mucus is noticeably increased and it is filled with tissue cells in various stages of disintegration. Frequently, as shown in figure 76, such cells may be partially surrounded by closely attached trophozoites, but whether this occurred before or after the cell became detached from the epithelium, it is impossible to say. Many trophozoites, however, lie free in the mucus, probably moving slowly about by means of pseudopodia. It is evident that when the parasites are abundant the gills may be seriously injured and in one extreme case the ends of several adjoining filaments were entirely destroyed, the space being occupied by mucus filled with trophozoites and disintegrating tissue cells.

The food and nutrition of the parasite present an interesting problem. Other species of Myxosporidia live in the tissues or in cavities of the host, such as the gall and urinary bladders, and consequently, are surrounded by fluids containing nutritive substances, which they presumably absorb. There are, however, several instances (Davis 1916, p. 336) where myxosporidian trophozoites have been observed to ingest solid food particles so that this method of feeding is not impossible. Nevertheless, no evidence has been found that this occurs in *C. externum*, although special attention has been paid to this possibility. We must assume, therefore, that the only nutrient the trophozoites obtain is absorbed in liquid form from the surrounding medium. The surface of the gills, which are continually bathed by flowing water, would seem to afford little opportunity for the accumulation of nutritive fluids. However, it is possible that the mucus may have a tendency to retain such substances. Furthermore, it seems probable that trophozoites in close contact with the epithelium may absorb directly, products produced by lysing the cells and that the condition shown in figure 76 is not simply for support. On the contrary, the primary purpose may be to digest the cell to which the trophozite is attached. It is common to find trophozoites clinging to epithelial cells in various stages of disintegration although most of them do not enclose the cells as closely as shown in the figure.

General Discussion

One of the most interesting problems in connection with *C. externum* is the obvious fact that here we have a reversal of the usual course of evolution, although there is evidence that it may have occurred in other groups such as the nematodes. So far as the writer is aware, however, no other case of a similar change in its mode of life is known among the Protozoa.

It is interesting to find that within the Myxosporidia there are species which indicate how this transformation from an internal to an external parasite may have been brought about. Although most myxosporidians found on the gills are cyst-forming, this is not true of all species: *Myxosoma endovosa* occurs only in the form of ameboid trophozoites similar to those of *C. externum*. In this species, however, the trophozoites are found in the capillaries of the lamella in which they sporulate. The trophozoites of a second species *Myxobilatus* (Henneguya) *plasmodia* (Davis 1922) leave the capillaries and move about among the cells of the respiratory epithelium. However, as shown in figure 85, this species does not normally come into contact with the water which bathes the gills, although the epithelial cells covering the trophozoites may be stretched to a very thin envelope. In exceptional cases the enclosing membrane may be stretched to the breaking point, but this condition cannot be considered normal. Finally, the next step is illustrated by

C. externum, which has left the respiratory epithelium and the protection it affords in favor of an existence on the surface of the gill.

Family **Myxosmatidae** Poche

Myxosoma endovasa, n. sp.

[Plate 7, figs. 81, 84, and 86]

While examining sections of the gills of a smallmouth buffalo (*Ictiobus bubalus*) from the Mississippi River at Fairport, Iowa, small trophozoites of a myxosporidian were found in the capillaries of the lamellae. Both vegetative and sporulating trophozoites were abundant and it was evident that this species, unlike other myxosporidians, spends most of its life in the blood vessels.

The trophozoites usually occurred in the large capillary extending around the edge of the lamella. Their relation to the capillary could best be seen in cross sections of the lamella (fig. 84). In such sections the trophozoites were roughly crescent shaped with the convex side of the organism toward the edge of the lamella and in close contact with the capillary wall. On the concave side of the trophozoite blood corpuscles could frequently be seen and it was evident that at first the capillary was not completely blocked by the trophozoite and that the blood continued to circulate past the concave side. This was made possible by distension of the capillary and consequent thinning of the wall so that it was very difficult to distinguish. It is probable that the larger sporulating trophozoites (fig. 86) may eventually stop the movement of blood in the capillary.

The trophozoite is composed of a thin, dense layer of ectoplasm surrounding the finely granular endoplasm which contains a larger number of nuclei. The vegetative nuclei are larger with a nucleolus, and with the chromatin granules more distinct than in the smaller generative nuclei. No specially differentiated layer of cytoplasm can be distinguished around the latter until they become segregated to form the sporoblasts. The trophozoites are polysporous.

When viewed from above, the spore is nearly spherical and contains two relatively large pyriform polar capsules. The shell valves are thin and without markings. Spores preserved in formalin were about 9μ long with a width of 8μ. The polar capsules were 3.5 by 5μ.

Order HAPLOSPORIDIA Caullery and Mesnil

Dermocystidium salmonis, n. sp.

[Plate 6, figs. 59–66; plate 14, figs. 210–213]

The gills of an adult chinook salmon (*Oncorhynchus tschawytscha*) from the Sacramento River at Balls Ferry, Calif., and confined for several weeks in a holding pond at the Coleman hatchery, showed a number of small, white cysts on the filaments. As they closely resembled myxosporidian cysts, it was assumed at first that they were formed by a member of this group. This was soon disproved by an examination of the contents. Although the cysts were filled with spherical bodies about the size of myxosporidian spores, the resemblance was only superficial, the internal structure being very different. Instead of the conspicuous polar capsules the greater part of each spore was occupied by a large, rounded refringent body which is the distinguishing character of the genus *Dermocystidium*.

Several species of this genus have been described from fish and amphibians in Europe, but none have been reported previously from this country. Two of the four European species occur in the skin of frogs and salamanders while the other two species are fish parasites. Dunkerly (1914) found the cysts of a *Dermocystidium* on the gills of the brown trout (*Trutta fario*) in Ireland which he believed was identical with a species previously described by Perez from salamanders.

A little later, Leger (1914) found the same parasite on gills of trout in the Alps. He showed that the species is distinct from that on salamanders and called it *Dermocystidium branchialis*. Recently Jirovec (1940) has described another species *D. vejdovskyi* which occurs on the gills of *Esox lucius*. This species differs in several respects from that found on trout, especially in the structure of the cysts. Jirovec believes that a parasite of *Daphnia magna* described by Ruhberg (1933) should be included in the genus.

There is no doubt that the species found on salmon is distinct from any of the European forms and con-

sequently the name *Dermocystidium salmonis* is proposed for it. Unfortunately, only preserved material was available for study.

The cysts (fig. 210) are located on the sides of the gill filaments where they occupy a cup-shaped cavity between the lamellae. They are rounded, glistening white and may reach a diameter of one millimeter. The mature cysts are easily dislodged from the gills and then can be seen to be composed of a thin transparent membrane surrounding a mass of spores. The loose connection of the cysts with the gill tissues sharply differentiates them from myxosporidian cysts which are attached more firmly. In section (fig. 212) the cyst wall can be seen in close contact with epithelial cells which surround it on all sides. From a study of young cysts (fig. 213) it appears that they develop in the thick epithelial layer between the bases of the lamellae. As the cyst grows the epithelial cells increase and there is also some hyperplasia in the epithelium of adjoining lamellae. This results in fusion of the lamellae to form the characteristic cup surrounding the cyst (fig. 211). Sometimes not more than three or four lamellae on each side are involved, in other cases as many as ten or twelve lamellae may be affected. Even the fully matured cyst is entirely surrounded by epithelial cells, although on the outer side they may be stretched to a single layer of thin, flattened cells. In sections, the cyst wall is more or less wrinkled and distorted, evidently due to shrinkage in the course of preparation.

In fully matured cysts the contents are composed of spherical spores, each containing a large, rounded body which in formalin material is homogeneous and highly refringent. The spores (fig. 66) vary considerably in size, the majority being about 8 to 10μ in diameter, but a few may reach a diameter of 12μ. The rounded body within the spore is about 6 to 7μ in diameter. Each spore is surrounded by a thin, transparent, structureless membrane without markings of any kind. The rounded body is always located excentrically, the wider space between the body and the spore wall being occupied by the nucleus surrounded by cytoplasm which in this region is denser than in other parts of the spore. The nucleus is of the vesicular type with a large deeply stained karyosome surrounded by a clear halo. The rounded body stains deeply with plasma stains such as eosin and Bordeaux red. It does not stain with Sudan III and stains a light pink with scarlet R. It fails to give the reaction for glycogen in Lugol's solution.

In two instances young cysts were found in which spores had not yet developed. One was only 60μ in diameter (fig. 213) with a comparatively small number of cells; the other was somewhat larger. Both cysts contained only loose, rounded cells. Each cell contained one or two nuclei (figs. 59–64) and was completely separated from its neighbors. There was nothing resembling a multinucleate plasmodium such as was found in *D. vejdovskyi* by Jirovec. The cells appeared to be multiplying rapidly, the nucleus first dividing to form a binucleate cell (figs. 62 and 63) which later divided into two equal parts (fig. 65). Several dividing binucleate cells were observed, but no case of nuclear division could be found. With the exception of the number of nuclei, the cells all showed the same structure. The cytoplasm was vacuolated with a central nucleus containing a large rounded karyosome. The karyosome appeared to be surrounded by achromatic material which was more abundant on one side and extended in strands to the nuclear wall.

All other cysts were much larger and the bulk of the contents was composed of fully developed spores. In several cysts there were certain areas containing cells which were evidently developing into spores. Various stages in the transformation of sporoblasts into spores (fig. 212) could be found without difficulty. The smallest sporoblast contained a central nucleus surrounded by granular vacuolated cytoplasm and were similar to the cells in young cysts, but smaller. Somewhat larger cells contained one or two—sometimes more—small, rounded, refringent bodies which are the forerunners of the large spheroidal bodies in the mature spore.

The history of the spores after leaving the cyst is unknown. A number of free spores were noticed on the gills which had evidently become entangled in the mucus, but they were in the same condition as when they left the cyst.

Since only the encysted stage of the various species of *Dermocystidium* is known and the structure of the spore is essentially the same in all, it is evident that characters for distinguishing the different species are very limited. Nevertheless, there can be little doubt that *D. salmonis* is specifically distinct from the European species. In *D. branchialis* the spore is smaller, with a diameter of 7μ to 8μ. The most marked difference, however, is in the character of the cyst wall, which is much thicker than in *D. salmonis*. Furthermore, there is no such regular arrangement of the lamellae surrounding the cyst. Also, according to Dunkerly,

the protoplasm in the cyst is only indistinctly divided into cells, which later become the sporoblasts. In *D. vejdovskyi* there is an even greater difference in the structure of the cyst, which is divided by a thin structureless membrane into numerous compartments, each containing one or more multinucleate plasmodia. The latter divide into uninucleate sporoblasts which develop into spores much as in *D. salmonis*.

There is much difference of opinion regarding the affinities of the genus. Alexeieff and Grassi have suggested a relationship to *Blastocystis*, but this appears to be based on a superficial resemblance rather than the possession of any fundamental characters in common. Leger, on the other hand, links *Dermocystidium* with the Haplosporidia which is such a heterogeneous group with indefinite limitations that it can easily be stretched to accommodate almost any taxonomic orphan. To the author it appears fruitless to speculate about the affinities of the genus until something is known regarding other stages in the life cycle.

CONTROL MEASURES

The control of ectoparasitic Protozoa presents no serious problem when fish are held in tanks or small pools, but in large ponds or under natural conditions little can be done to reduce their numbers. The most practicable method of control is to place the fish in a solution which will kill the parasites without material injury to the host. A number of chemicals have been used for this purpose, the most common being salt and acetic acid. Immersion of the fish in a 3 percent solution of salt (sodium chloride) for 3 to 10 minutes will kill or so weaken most protozoans that they will leave the host. A more effective treatment, however, is to dip the fish in a 1 to 500 solution of glacial acetic acid. Both of these methods necessitate considerable handling of the fish which, especially when several treatments are required, may be quite injurious. Furthermore, when large numbers of fish are to be treated the dipping method requires much time and labor.

Recently Fish (1940, 1940a) has developed a formalin treatment, especially designed for use in raceways and small pools, which is the most effective means yet devised for ridding fish of ectoparasitic Protozoa. In this treatment the fish are held for 1 hour in a solution composed of 1 part formalin (40 percent formaldehyde) to 4,000 parts water. The formalin is added directly to the tank or pool containing the fish. Since it diffuses very slowly through the water, special precautions must be taken to obtain a uniform concentration. An effective method is to dilute the formalin 1 to 100 and then spread the solution as uniformly as possible over the surface of the water. If the fish are crowded it will be necessary to aerate the water during treatment. This treatment will kill all external protozoans and will not injure the fish appreciably unless they have already been greatly weakened by the parasites.

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EXPLANATION OF PLATES

Plates 1 to 7 are from figures by the author, drawn to scale with the aid of the camera lucida. Plates 7 to 14 are from photomicrographs by the author. The approximate magnification is given for each figure.

ABBREVIATIONS

ad. s., adoral spiral

ba., bacteria

bl., blepharoplast

b. m., border membrane

c. g., ciliary girdle

cil., cilia

cp., cytopharynx

c. v., contractile vacuole

c. v. d., duct from contractile vacuole

dt., denticle

fl., flagellum

la., gill lamella

m., mouth

ma., macronucleus

mb., membranelle

m. c., marginal cilia

mi., micronucleus

mng., macronuclear anlagen

my., myoneme

n., nucleus

p. b., peristome border

scp., scopula

st., stigma

st. b., striated band

tr., trichites

ve., velum

vt., vestibule

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ILLUSTRATIONS

724094—47——3

PLATE 1

FIGURES 1–4.—Free-swimming individuals of *Colponema agitans*. The nucleus and elongated blepharoplast are deeply stained. × 2,500.

FIGURE 5.—Three individuals of *C. agitans* attached to gill epithelium. Drawn from section. × 2,500.

FIGURE 6.—*Bodomonas concava* attached to gill epithelium by posterior flagellum. × 2,500.

FIGURE 7.—*B. concava* attached to epithelial cell in position usually found when first placed on slide. Drawn from whole mount. × 2,500.

FIGURE 8.—Side view of *C. agitans* attached to epithelium. Drawn from section. × 2,500.

FIGURE 9.—Attached form of *B. concava* viewed from flattened ventral side. The blepharoplast is in thinner part of body. × 2,500.

FIGURE 10.—Group of *B. concava* attached to epithelium in usual position. Drawn from section. × 2,000.

FIGURES 11–13.—Free-swimming specimens of *B. concava*. Drawn from whole mount. × 2,500.

FIGURE 14.—Living *B. concava* attached to gill. × 2,500.

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PLATE 2

FIGURE 15.—Free-swimming form of *Lamellasoma bacillaria*. × 2,500.

FIGURE 16.—Attached form of *L. bacillaria* viewed from the side. Drawn from unstained specimen killed in osmic vapor. × 1,340.

FIGURE 17.—Attached form of *L. bacillaria* viewed from above. × 2,500.

FIGURE 18.—Free-swimming form of *L. bacillaria* drawn from unstained specimen killed in osmic vapor. × 1,340.

FIGURES 19 and 20.—*Euglenosoma branchialis* to show spiral twist to body and ventral groove. Internal structure is not shown. × 2,000.

FIGURES 21 and 23.—Free-swimming form of *E. branchialis*. × 2,500.

FIGURE 22.—*E. branchialis* attached to gill epithelium. × 2,500.

FIGURE 24. Section of *Amphileptus voracus* through mouth. Only one macronucleus in section.

FIGURE 25. *A. voracus*, drawn from specimen preserved in formalin. × 1,000.

FIGURE 26. Section of *A. voracus* showing both macro- and micronuclei. × 1,000.

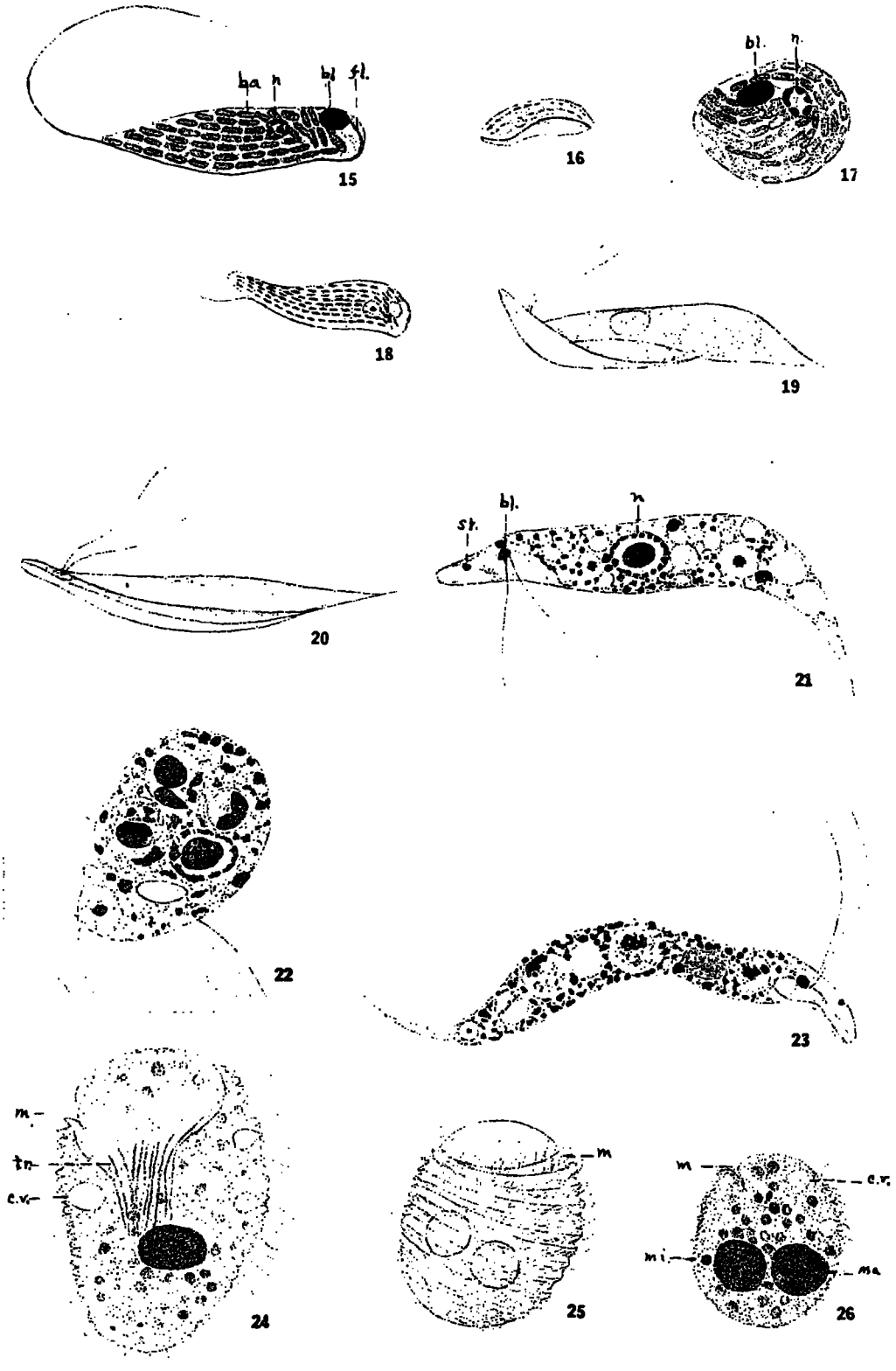
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PLATE 3

FIGURE 27.—Section of *Trichodina discoidea* through mouth. × 1,340.

FIGURE 28.—Part of denticulate ring, *T. discoidea*. × 2,000.

FIGURES 29 and 30.—Sections of *T. discoidea*. × 1,340.

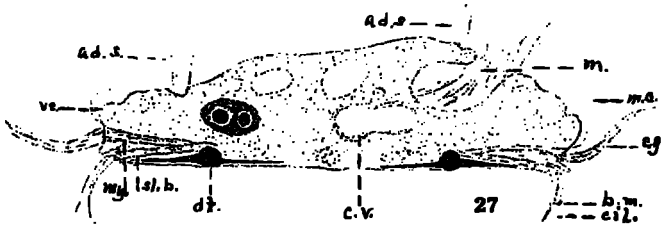
FIGURE 31.—Section of *T. bulbosa*. × 1,340.

FIGURE 32.—Section of *T. vallata*. × 1,340.

FIGURE 33.—*T. bulbosa* viewed from side with adoral spiral. Drawn from whole mount. × 670.

FIGURE 34.—Section *T. platyformis*. × 1,000.

FIGURE 35.—*T. bulbosa*, seen from opposite side to that shown in figure 33. × 670.



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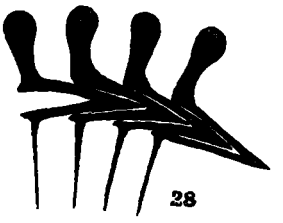
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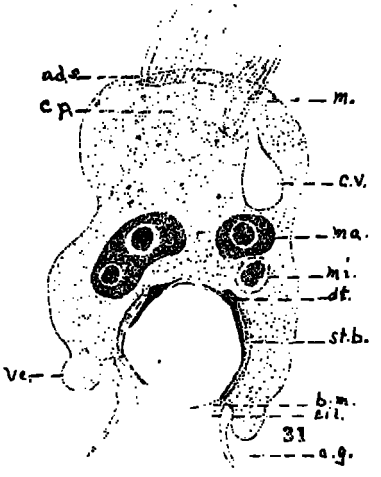

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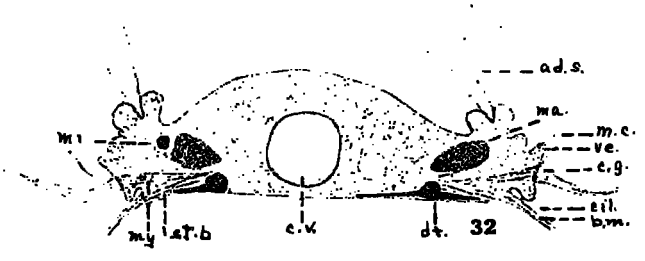

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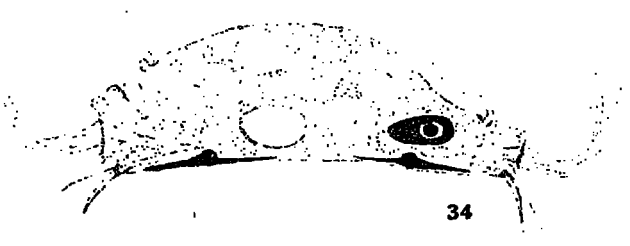
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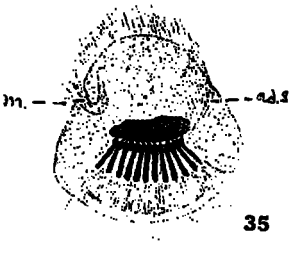

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PLATE 4

FIGURE 36.—Section of *Trichodina tumefaciens* through mouth. × 1,340.

FIGURE 37.—Section of *T. tumefaciens* showing usual shape of body. × 1,340.

FIGURE 38.—Side view of *T. bursiformis* drawn from whole mount. × 1,340.

FIGURE 39.—Section of *T. californica*. An epithelial cell is being taken into the mouth. × 1,000.

FIGURE 40.—Section of *T. bursiformis*. × 1,340.

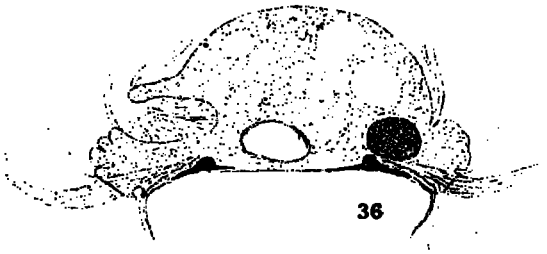
FIGURE 41.—Section of *T. californica* with flattened adoral surface. × 1,000.

FIGURE 42.—Side view of *T. bursiformis*. Drawn from unstained specimen killed in osmic vapor. × 670.

FIGURE 43.—Section of *T. californica* with bulk of body on one side of adhesive disk. × 1,000.

FIGURE 44.—Part of denticulate ring of *T. bursiformis*. × 2,000.

FIGURE 45.—Part of denticulate ring of *T. californica*. × 2,000.



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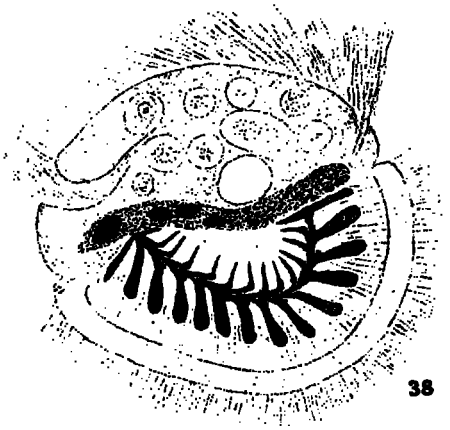

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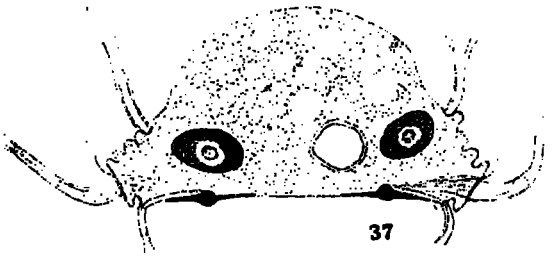

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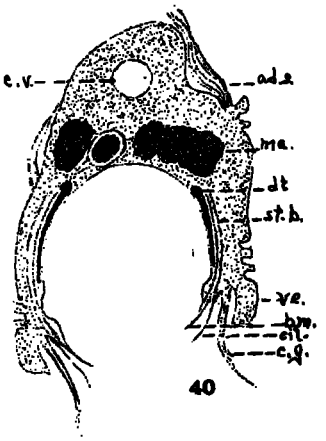

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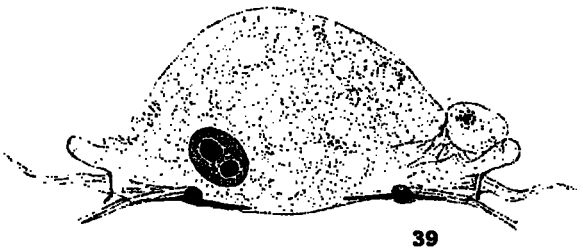

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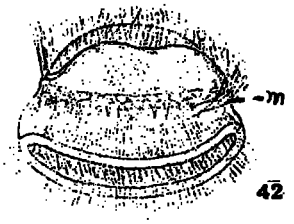

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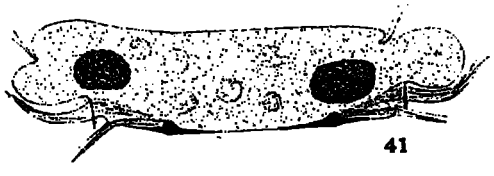

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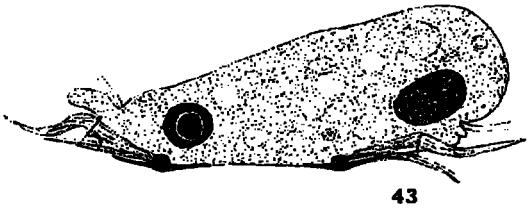

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PLATE 5

FIGURES 46 and 48.—Sections through part of body of *Trichodina fultoni*. × 1,340.

FIGURE 47.—Section through body of *T. fultoni*. Note food vacuole containing epithelial cells. × 670.

FIGURES 49, 50, and 51.—Sections of *T. symmetrica*. In fig. 50 the micronucleus can be seen by the side of the macronucleus with the contractile vacuole on the other side. × 1,340.

FIGURE 52.—Section of *T. symmetrica* through mouth. Such extreme distension of the cytopharynx is very unusual. × 1,340.

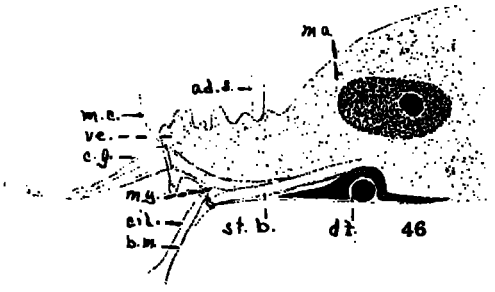
FIGURE 53.—Part of denticulate ring, *T. truttae*. × 1,000.

FIGURE 54.—Part of denticulate ring *T. fultoni*. × 1,000.

FIGURES 55 and 56.—Sections of *T. myakkae*. × 1,340.

FIGURE 57.—Adoral view of *T. myakkae*. × 1,340.

FIGURE 58.—Part of adhesive disk of *T. myakkae*, Semi-diagrammatic. × 2,000.



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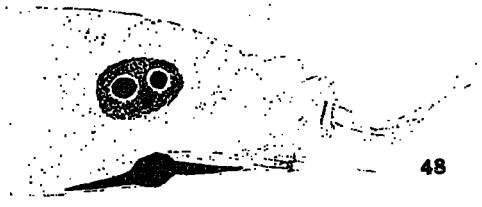
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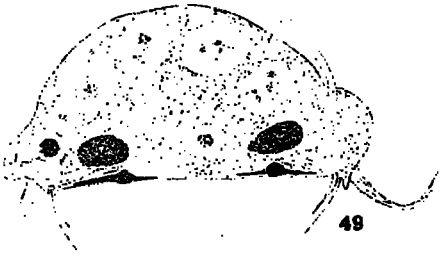
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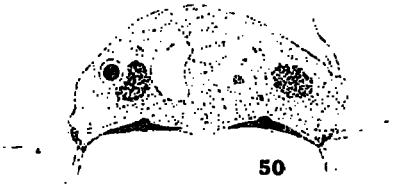
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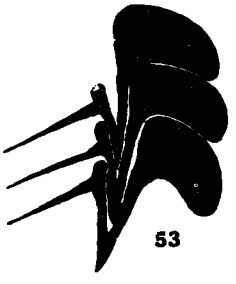
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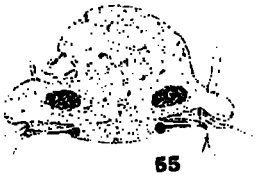
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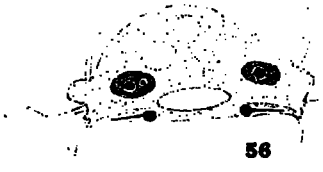
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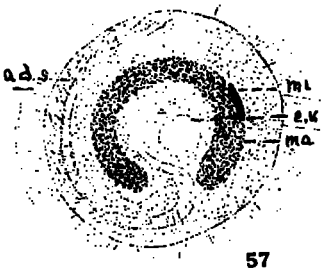

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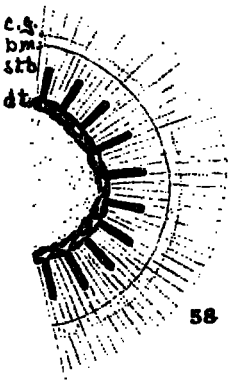

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PLATE 6

FIGURES 59–63.—Cells from young cyst of *Dermocystidium salmonis*. × 2,500.

FIGURE 64.—Developing spore of *D. salmonis*. Drawn from formalin material. × 1,340.

FIGURE 65.—Dividing binucleate cell of *D. salmonis*. × 2,500.

FIGURE 66.—Mature spore *D. salmonis*. × 2,500.

FIGURE 67.—Adoral view of peristome of *Scyphidia macropodia*. Semi-diagrammatic. × 1,340.

FIGURE 68.—Small form of *S. macropodia* with micronucleus in anaphase. × 1,000.

FIGURE 69.—*S. macropodia*. Drawn from whole mount. × 1,000.

FIGURE 70.—Section of *S. macropodia* during conjugation. The microconjugant has 8 micronuclei, the macroconjugant, 4 micronuclei. × 1,000.

FIGURE 71.—Section of expanded *S. macropodia*. Part of the macronucleus was in the next section. × 1,000.

FIGURE 72.—Section of *S. macropodia* through vestibule. Only part of macronucleus is shown. × 1,000.

FIGURE 73.—Section of *Trichophrya ictaluri* attached to lamella. The parasite is in contact with the capillary network which forms the middle layer of the lamella. The epithelium on the opposite side of the lamella is not shown. × 1,340.

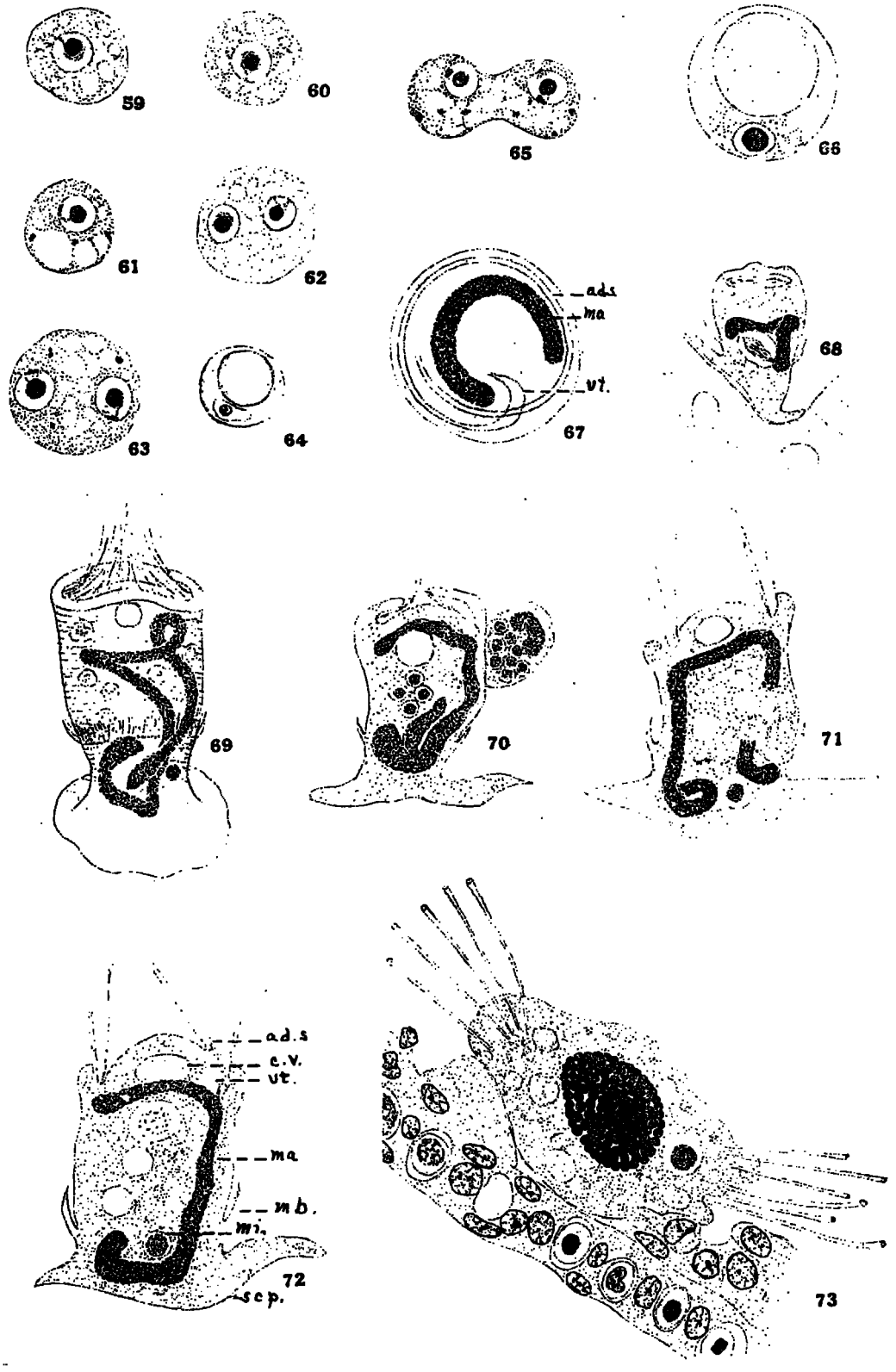
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PLATE 7

FIGURE 74.—Trophozoite of *Chloromyxum externum*. The granular endoplasm is surrounded by the hyaline ectoplasm. Drawn from living organism. × 1,340

FIGURE 75.—Similar to figure 74, but drawn from a stained specimen. Each generative nucleus is surrounded by a dense layer of cytoplasm. × 1,340.

FIGURE 76.—Trophozoite of *C. externum* closely attached to epithelial cell. × 1,340.

FIGURE 77.—Sporulating trophozoite of *C. externum* with two spores, one not yet fully developed. × 1,340.

FIGURE 78.—Trophozoite of *C. externum* attached to epithelium of lamella. The epithelial cells are disintegrating. × 1,340.

FIGURE 79.—Trophozoite of *C. externum* more highly magnified. × 2,500.

FIGURE 80.—Spore of *C. externum* viewed at right angles to sutural plane. × 1,340.

FIGURE 81.—Spore of *Myxosoma endovasa*. × 1,340.

FIGURE 82.—Trophozoite of *C. externum* in epithelium at edge of lamella. × 1,340.

FIGURE 83.—Trophozoite of *C. externum* attached to epithelium of gill filament × 1,340.

FIGURE 84.—Cross section of edge of gill lamella showing trophozoite of *Myxosoma endovasa* in capillary. × 1,340.

FIGURE 85.—Section of lamella with trophozoite of *Myxobilatus plasmodia* in epithelium. × 1,340.

FIGURE 86.—Section of edge of lamella showing capillary with vegetative and sporulating trophozoites of *M. endovasa*. × 1,340.

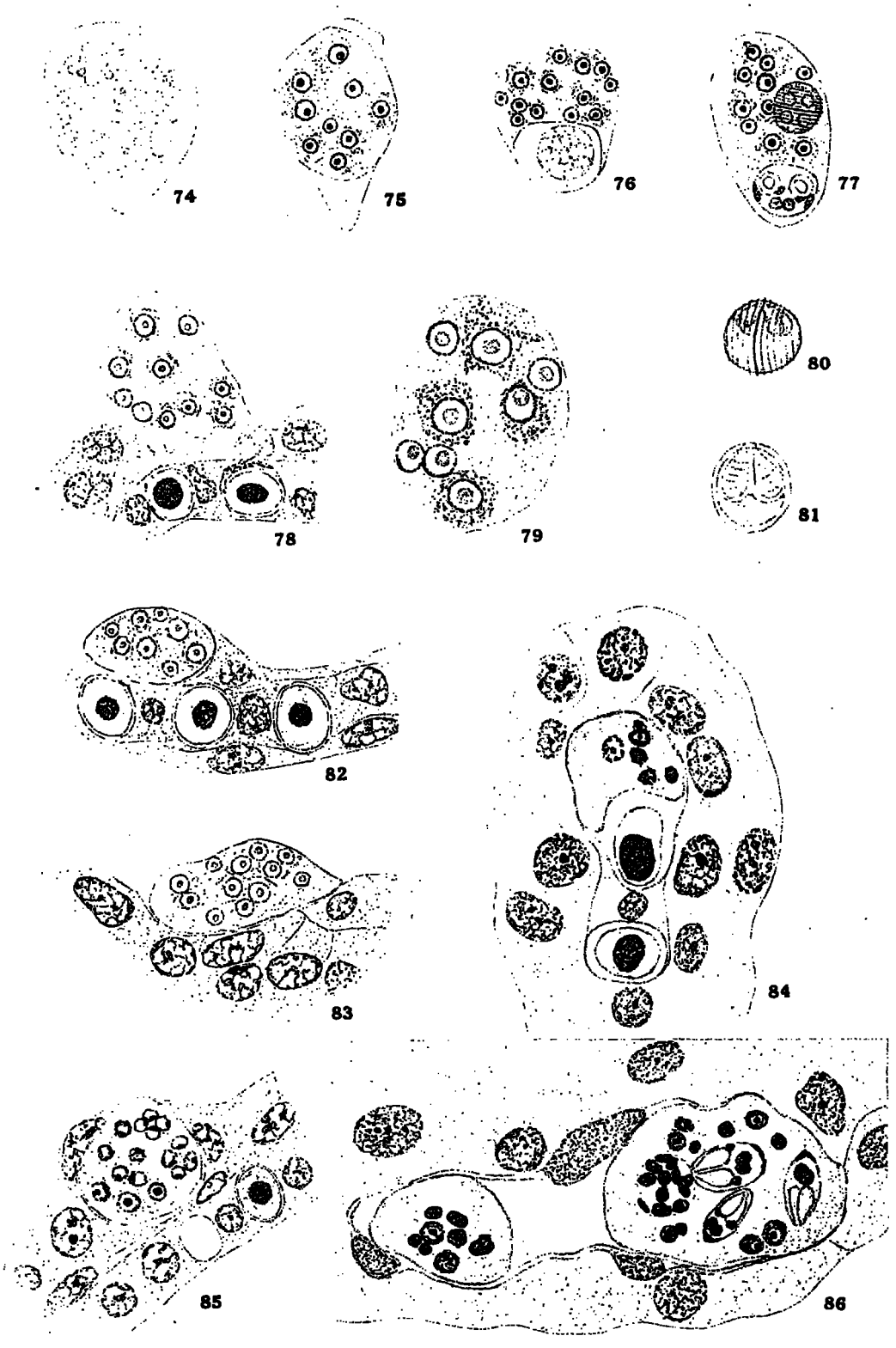
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PLATE 8

FIGURE 87.—Section of gill epithelium infected with *Bodomonas concava*. × 1,270.

FIGURES 88 and 89.—Sections of gill epithelium infected with *Colponema agitans*. × 1,270.

FIGURES 90, 94, and 95.—Free-swimming form of *Lamellasoma bacillaria*. From whole mounts. × 1,270.

FIGURE 91. *L. bacillaria* attached to epithelial cell. From whole mount. × 1,270.

FIGURES 92 and 93. Attached form of *L. bacillaria* viewed from side. From whole mounts. × 1,270.

FIGURE 96. Attached form of *L. bacillaria* viewed from above. From whole mounts. × 1,270.

FIGURES 97 and 98. *Euglenosoma branchialis*. From whole mounts. × 1,270.

FIGURE 99.—Section of *Amphileptus voracus* nearly surrounded by epithelial cells. Only one macronucleus is shown. × 680.

FIGURE 100. Section of *A. voracus* which has just ingested a trichodinid. The endoplasm is filled with metaplastic bodies. × 680.

FIGURE 101.—Section of *A. voracus* showing small micronucleus at end of macronucleus. × 680.

FIGURE 102. Section of *A. voracus* showing concentric ridges on upper side. × 680.

FIGURE 103. Section of *A. voracus* showing macronuclei just beginning to divide. The organism has already divided into two daughter cells, but this is not visible in photograph. × 680.

FIGURE 104. Later stage in division of macronucleus. × 680.

FIGURE 105. Section of *A. voracus* attached to lamella showing both macronuclei in resting stage. × 680.

FIGURE 106.—Section of one side of body of *A. voracus* showing ridges running in two directions. × 680.

FIGURE 107.—Whole mount of *A. voracus*. × 680.

FIGURE 108.—Section of *A. voracus* showing one end of organism with mouth opening and transverse ridges containing trichocysts. × 680.

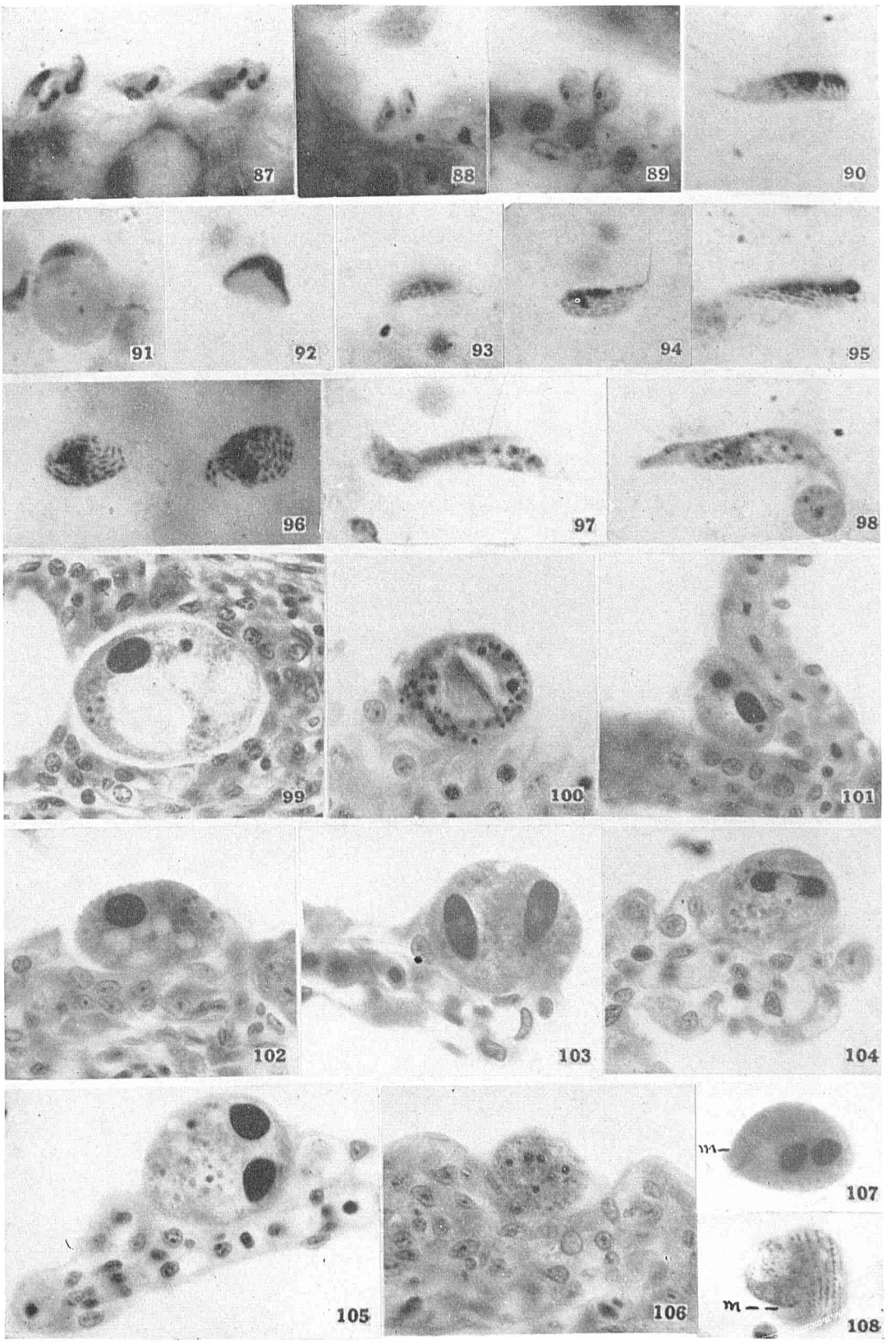
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PLATE 9

FIGURE 109.—Adhesive disk of adult *Trichodina discoidea* showing denticulate ring encircled by striated band. Outside the striated band is the faintly striated border membrane. × 680.

FIGURE 110.—Adhesive disk of a somewhat younger stage of *T. discoidea*. Alternate bars in the striated band are less distinct and the hooks and rays of the denticles are more slender than in figure 109. × 680.

FIGURES 111 and 112.—Section of *T. discoidea* attached to gill epithelium. × 680.

FIGURES 113 and 114.—Adhesive disks of juvenile *T. discoidea*. The new bars in the striated band are just beginning to appear. × 680.

FIGURES 115 and 116.—Sections of *T. discoidea* on gills. × 680.

FIGURES 117 and 119.—Sections of *T. platyformis*. × 680.

FIGURE 118.—Section of *T. fultoni* showing duct from contractile vacuole to exterior. × 680.

FIGURE 120.—Section of *T. fultoni* ingesting an epithelial cell. × 680.

FIGURE 121.—Adhesive disk of adult *T. platyformis*. × 680.

FIGURE 122.—Adhesive disk of *T. fultoni*. × 510.

FIGURE 123.—Section of *T. vallata* showing extreme development of ridge bearing adoral spiral. × 680.

FIGURE 124.—Section of *T. vallata* with less prominent adoral ridge. × 680.

FIGURE 125.—Part of adhesive disk of *T. fultoni* to show structure of denticulate ring and striated band. × 680.

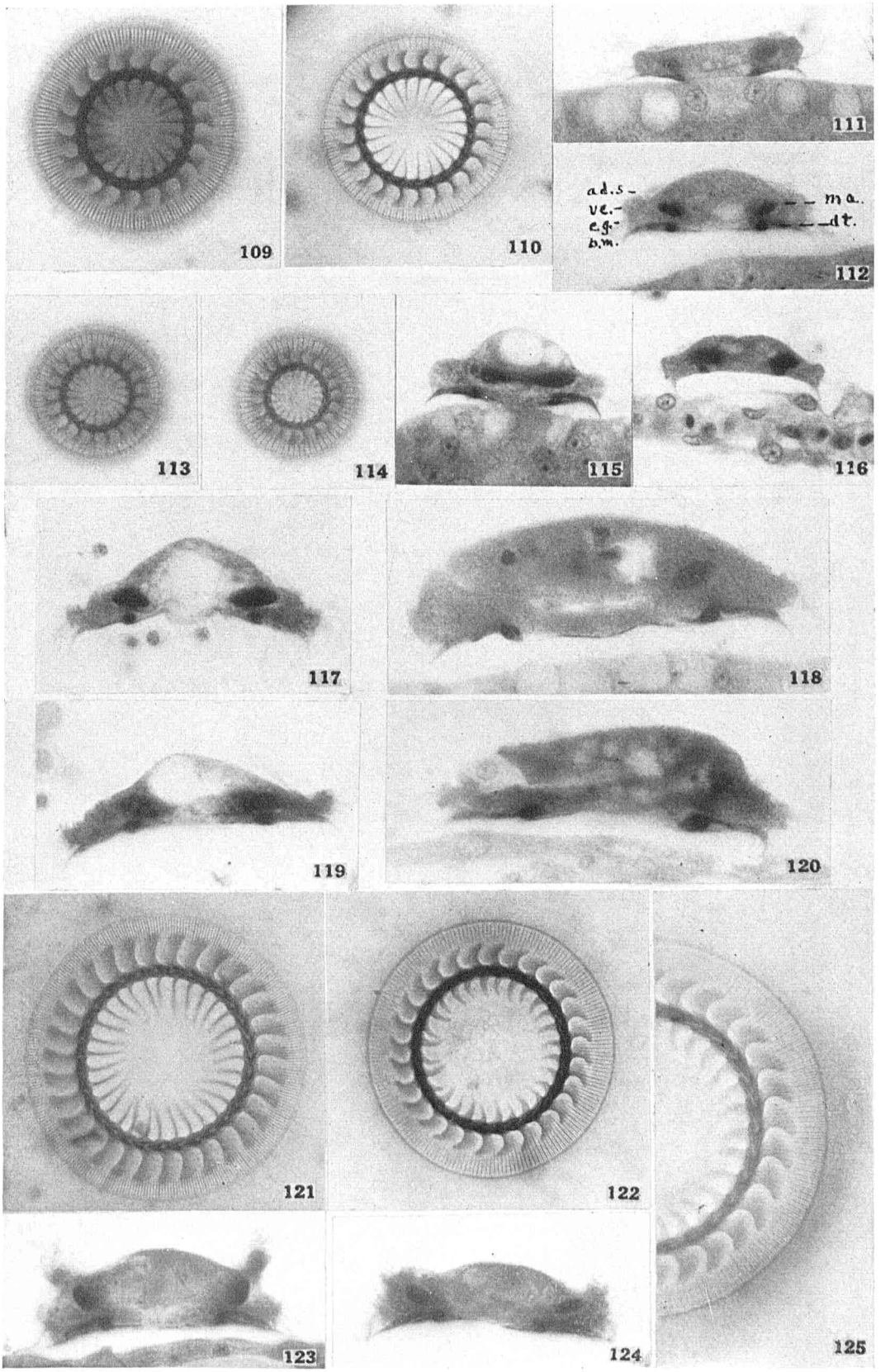
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PLATE 10

FIGURE 126.—Adhesive disk of *Trichodina vallata*. × 680.

FIGURE 127.—*T. fultoni* from adoral side to show separate openings of cytopharynx and duct from contractile vacuole. × 340.

FIGURE 128.—Part of adhesive disk of *T. platyformis* with lens focused just below striated band to show myonemes extending to ciliary girdle. × 680.

FIGURES 129 and 130.—Adhesive disks of *T. truttae*. × 340.

FIGURES 131 and 132.—Adhesive disks of *T. californica*. × 680.

FIGURE 133.—Surface view of *T. californica* covered by deposit of amorphous material. × 680.

FIGURE 134.—Adoral view of *T. symmetrica*. The small micronucleus can be seen near the lower arm of the macronucleus. × 680.

FIGURES 135 and 136.—Sections of *T. symmetrica*. × 680.

FIGURE 137.—Section of *T. californica* filled with amorphous material. The macronucleus has been broken across one arm. × 680.

FIGURES 138 and 139.—Adhesive disks of *T. symmetrica*. × 680.

FIGURE 140.—Section of normal *T. californica* through mouth opening. × 680.

FIGURES 141 and 142.—Sections of *T. tumefaciens*.

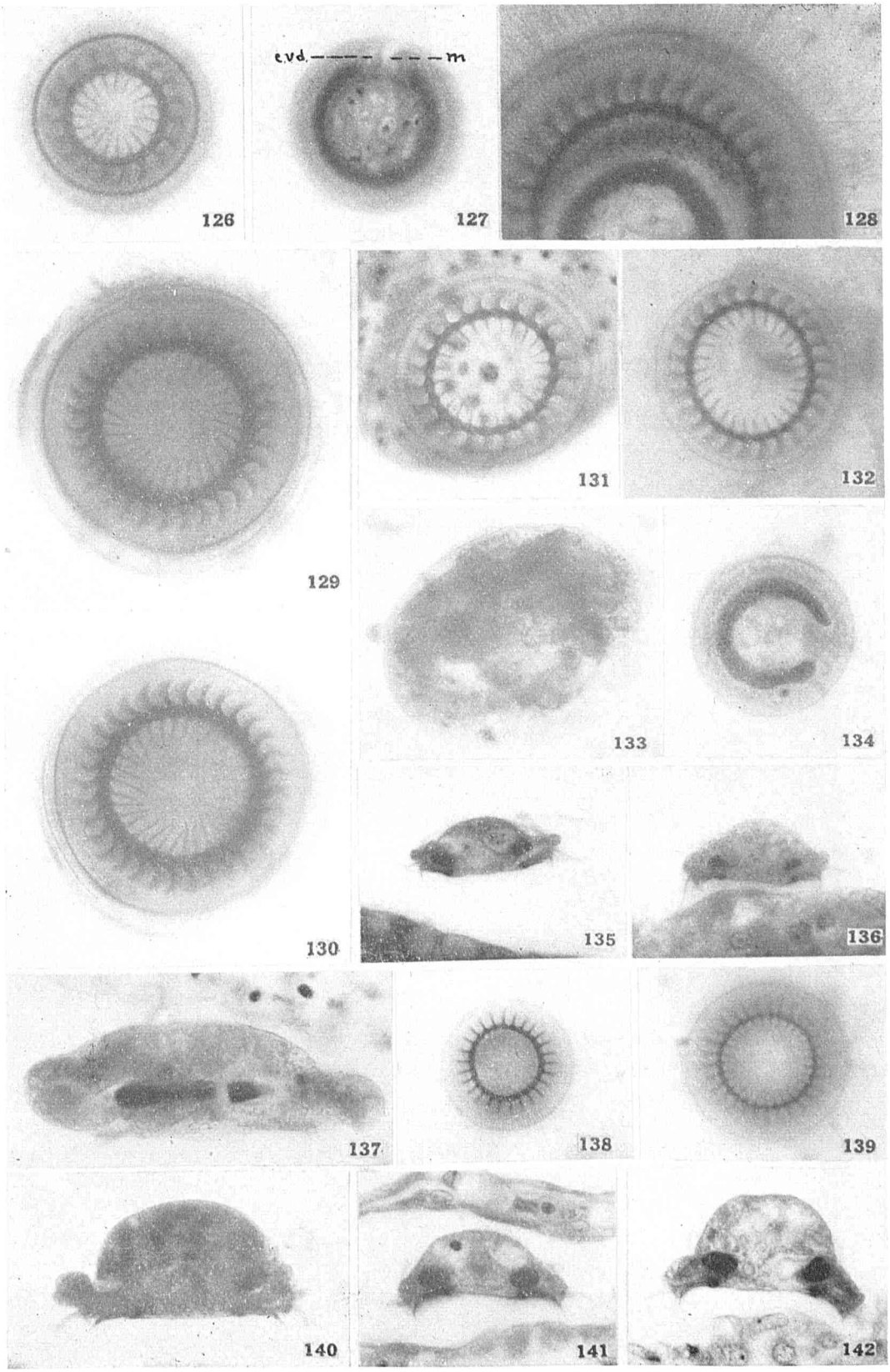
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PLATE 11

FIGURES 143 and 144.—Adhesive disks of juvenile *Trichodina tumefaciens*. × 680.

FIGURE 145.—Adhesive disk of intermediate stage, *T. tumefaciens*. × 680.

FIGURE 146.—Adhesive disk of adult *T. tumefaciens*. Hooks and rays of denticles are much broader than in earlier stages. × 680.

FIGURE 147.—Section of *T. tumefaciens* showing opening of contractile vacuole to exterior. The mouth is at a lower focus. × 680.

FIGURE 148.—Section of *T. tumefaciens* with most of body at one side of adhesive disk. × 680.

FIGURE 149.—Side view of *T. bulbosa* with adoral dome more elongate than usual. × 680.

FIGURES 150 and 151.—Adhesive disks of *T. bulbosa*. × 680.

FIGURE 152.—View of *T. bulbosa* from side showing adoral spiral. × 680.

FIGURE 153.—*T. bulbosa* from side opposite to that shown in figure 152. × 680.

FIGURES 154–157.—Sections of *T. bulbosa*. × 680.

FIGURE 158.—Adhesive disk of *T. bursiformis*. × 680.

FIGURE 159.—Side view of *T. bursiformis*. × 680.

FIGURES 160 and 161.—Sections of *T. bursiformis* attached to lamellae. × 680.

FIGURE 162.—*T. bursiformis* seen from side opposite to that shown in figure 159. × 680.

FIGURE 163.—Side view of *T. bursiformis* photographed at higher focus to show opening formed by edges of adhesive disk. × 680.

FIGURE 164.—Section of *T. bursiformis* attached to edge of lamella. × 680.

FIGURE 165.—*T. bursiformis* viewed from adoral side. The dark circle at a lower focus is the outline of the adhesive disk. × 680.

FIGURE 166.—Adhesive disk of *T. myakkae*. × 680.

FIGURES 167–169.—Sections of *T. myakkae*. × 680.

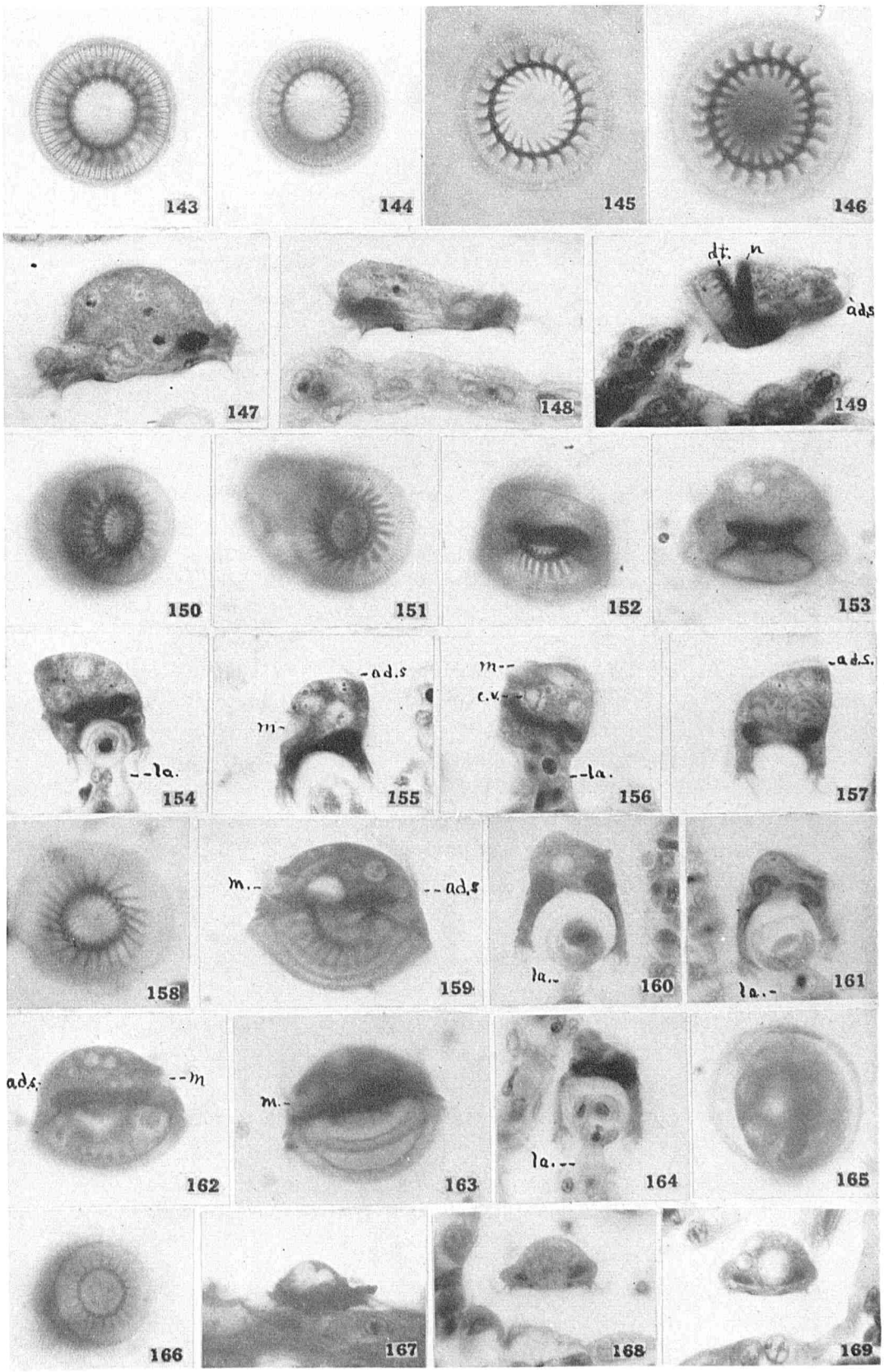
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PLATE 12

FIGURES 170–175.—Successive stages in division of the adhesive disk of *Trichodina fultoni*.

FIGURE 170.—Early stage, showing split in striated band, but denticulate ring not yet affected. The dark line in the striated band is the new denticulate ring formed of overlapping plates. × 510.

FIGURE 171.—Later stage showing division of denticulate ring. The dividing macronucleus can be seen indistinctly at a lower focus. × 510.

FIGURE 172.—Daughter individual formed by fission in which denticulate ring is just closing. × 510.

FIGURE 173.—Slightly later stage than figure 172. New denticulate ring of overlapping plates can now be seen clearly. The old ring is being resorbed. × 510.

FIGURE 174.—Later stage with old denticulate ring nearly resorbed. Hooks are forming on the new ring, but the rays have not yet appeared. × 510.

FIGURE 175.—Still later stage in which development of new denticulate ring is nearly completed. Remains of the old ring are still visible. The first indication of new bars can be seen in the striated band. × 510.

FIGURE 176.—Adhesive disk of *T. discoidea* in early stage of fission. × 680.

FIGURE 177.—Binary fission in *T. symmetrica* showing dividing macronucleus. Just below is the micronucleus in later stage of division. Photographed from section. × 680.

FIGURE 178.—Dividing micronucleus of *T. symmetrica*. The macronucleus in adjoining section formed a rounded mass, but had not yet started to divide. × 680.

FIGURES 179–181.—Formation of new denticulate ring in *T. discoidea* shortly after fission. × 680. Compare with figures 172 to 175.

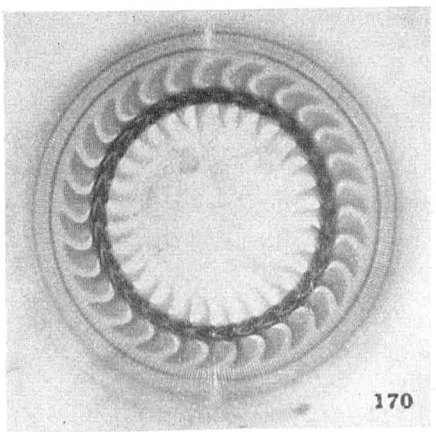
FIGURE 182.—Section of conjugating *T. discoidea* in early stage. The macronuclei have not yet begun to break down. × 680.

FIGURE 183.—Section of conjugating *T. tumefasciens* in same stage as figure 182. × 680.

FIGURE 184.—Section of conjugating *T. symmetrica* in same stage as above. × 680.

FIGURE 185.—Section of conjugating *T. bulbosa* at a somewhat later stage than in preceding figures. The macronuclei have now broken down into rounded bodies. × 680.

FIGURE 186.—Section of conjugating *T. discoidea* in late stage. A dividing micronucleus in late anaphase can be seen in lower coniugant. × 680.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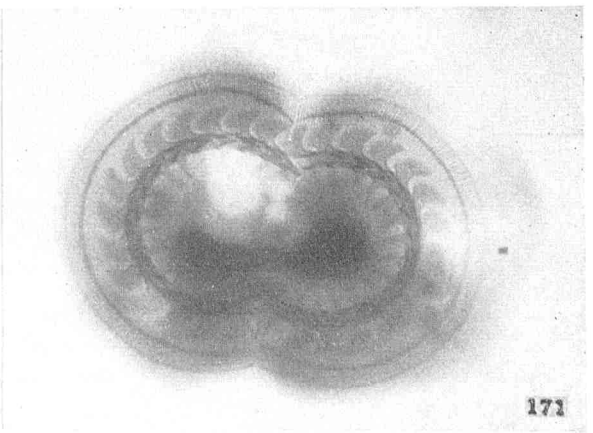
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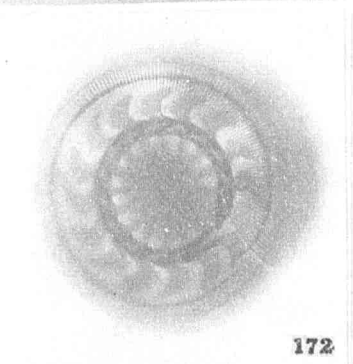
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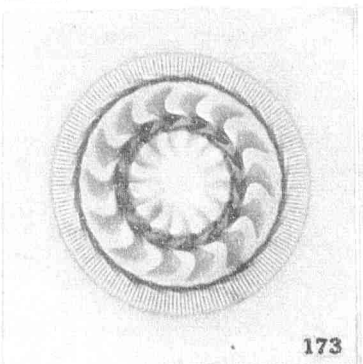
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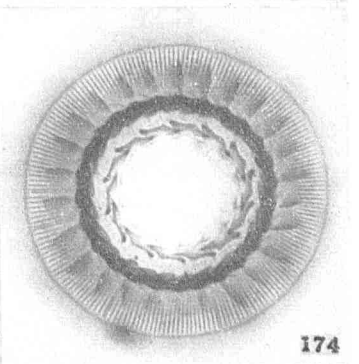
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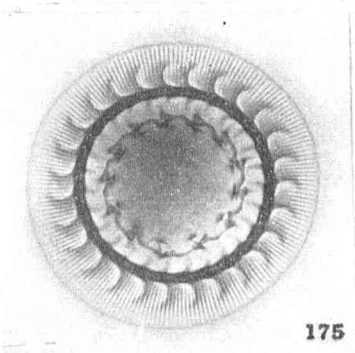
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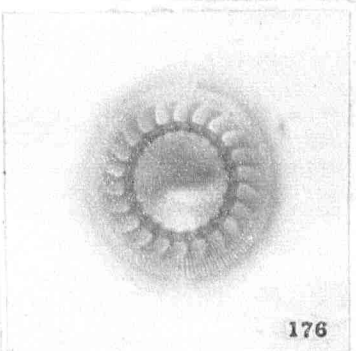
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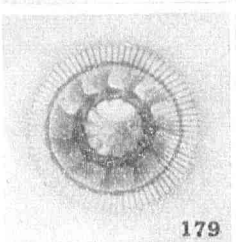
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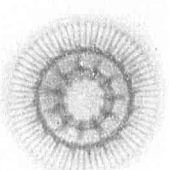
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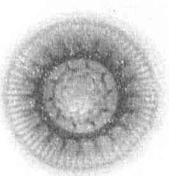
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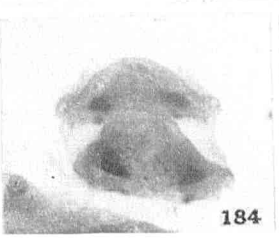
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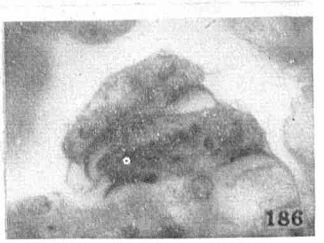
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PLATE 13

FIGURE 187.—Conjugating pair of *Trichodina discoidea* viewed from lower side. The smaller conjugant is plainly a juvenile. The dark line in the adhesive disk separates the striated brand from the border membrane, which is more distinct than usual. × 680.

FIGURE 188.—Conjugating pair of *T. discoidea* viewed from lower side. The lower conjugant (uppermost in photograph) is an adult, while the other is evidently a juvenile. The rudiments of a new denticulate ring can be seen in the striated band of each conjugant. × 680.

FIGURE 189.—One of a conjugating pair in *T. symmetrica* viewed from the adoral side. The macronucleus is becoming elongated with the formation of branches and will soon break up into rounded fragments. × 680.

FIGURES 190 and 191.—Exconjugants of *T. discoidea* in which a new denticulate ring is developing with the same number of denticles as the old. × 680. Compare with figures 172 to 181.

FIGURE 192.—Exconjugant of *T. tumefaciens* in which the macronuclear anlagen are just beginning to enlarge and become distinguishable among rounded fragments of the macronucleus. × 680.

FIGURE 193.—Exconjugant *T. symmetrica* with macronuclear anlagen clearly distinguishable. × 680.

FIGURES 194 and 195.—Photographs of exconjugant of *T. discoidea* taken at different levels. The adhesive disk in fig. 194 is evidently that of a juvenile. A new denticulate ring is forming with the same number of denticles as the old. At a lower focus macronuclear anlagen can be seen among the rounded fragments of the macronucleus. × 680.

FIGURE 196.—*T. discoidea* with two large macronuclear anlagen, the functional micronucleus, and rounded fragments of the original macronucleus. ×680.

FIGURE 197.—A later stage than figure 196 showing U-shaped macronucleus, micronucleus, and fragments of original macronucleus. × 680.

FIGURE 198.—Living *Scyphidia macropodia* attached to gill epithelium. × 340.

FIGURE 199.—Section of *S. macropodia* with retracted peristome. × 680.

FIGURE 200.—Section of *S. macropodia* with peristome expanded. × 680.

FIGURE 201.—Side view of living free-swimming telotroch stage of *S. macropodia*. × 340.

FIGURE 202.—Whole mount of telotroch stage viewed from above to show condition of macronucleus. × 680.

FIGURES 203 and 204.—Postconjugant of *S. macropodia* photographed at two levels to show macronuclear anlagen. × 680.

FIGURE 205.—*S. macropodia* dividing by binary fission. × 680.

FIGURE 206.—Living *S. macropodia* attached to gill filament. Two individuals of small form at extreme left. × 340.

FIGURES 207 and 208.—Postconjugants of *S. macropodia* with three macronuclear anlagen and functional micronucleus. × 680.

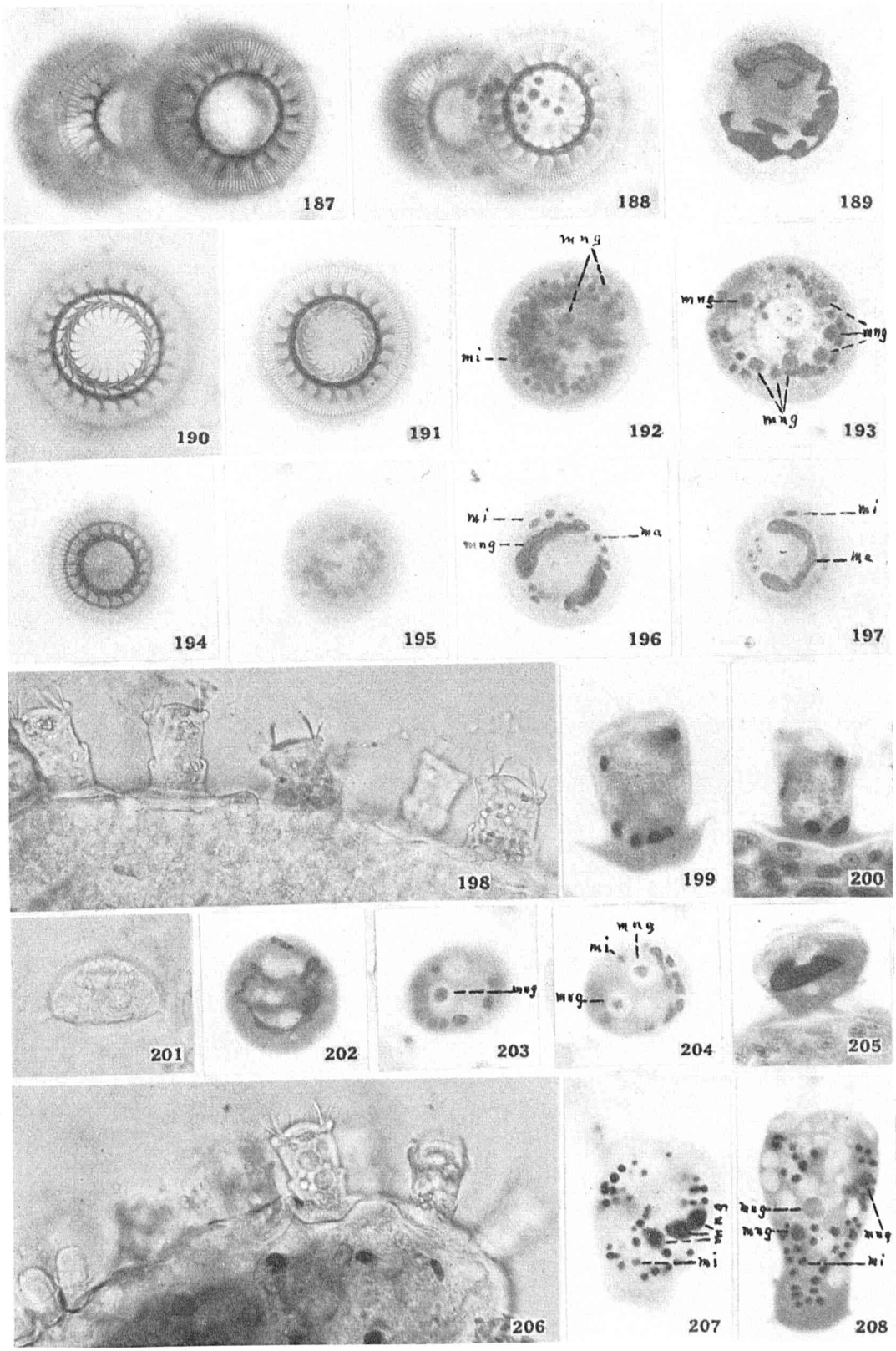
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PLATE 14

FIGURE 209.—Four small individuals of *Scyphidia macropodia* which are believed to have been formed by two successive divisions of postconjugant. The micronuclei are not shown. × 680.

FIGURE 210.—Cysts of *Dermocystidium salmonis* on gill filaments. ×7.

FIGURE 211.—Section of cyst of *D. salmonis* showing fusion of lamellae surrounding cyst. The space between the spores and the cyst wall is due to shrinkage. × 85.

FIGURE 212.—Section of part of cyst of *D. salmonis* showing sporoblasts and mature spores. The thin cyst wall is in close contact with epithelial cells. × 680.

FIGURE 213.—Section of young cyst of *D. salmonis*. The irregularities in the cyst wall are probably due to shrinkage. × 680.

FIGURE 214.—Adult *Trichophrya ictaluri* with four fascicles of tentacles. Photographed from unstained specimen preserved in formalin. × 510.

FIGURES 215 and 216.—Trophozoite of *Chloromyxum externum* attached to gills. × 680.

FIGURE 217.—Conjugation in *Scyphidia macropodia*. The micronuclei are dividing in both conjugants. × 680.

FIGURE 218.—Formation of microconjugant in *S. macropodia*. × 680.

FIGURE 219.—Exceptionally large trophozoite of *C. externum*. × 680.

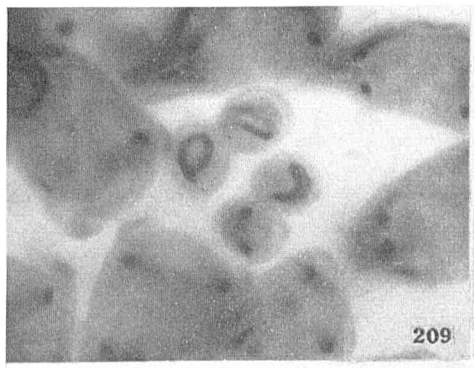
FIGURE 220.—Trophozoite of *C. externum* attached to lamella. Note that it appears to be continuous with the epithelium. × 680.

FIGURE 221.—Sporulating trophozoite of *C. externum*, containing a mature spore (deeply stained) and developing spore just above. × 680.

FIGURE 222.—Section of *Trichophrya ictaluri* attached to lamella. The endoplasm contains rounded metaplastic bodies in addition to the macronucleus. × 680

FIGURE 223.—Section of *T. ictaluri*. The epithelial cells have been destroyed or forced to one side, so that the parasite is in direct contact with the capillary network of the lamella. × 680.

FIGURE 224.—Section of gill of minnow showing several trophozoites of *C. externum*. × 680.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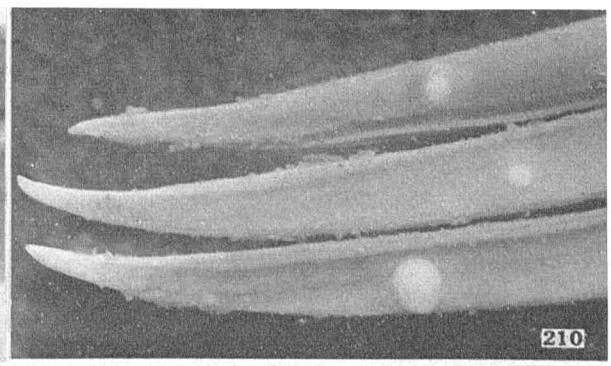
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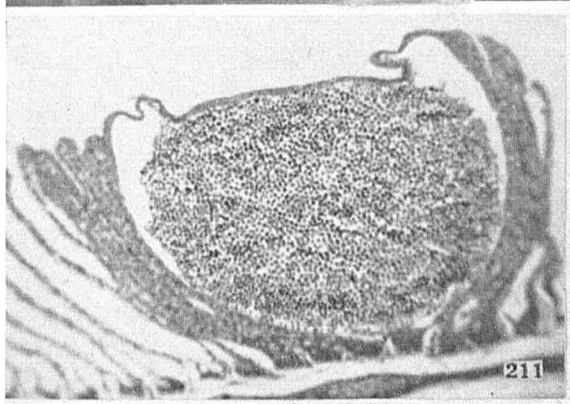
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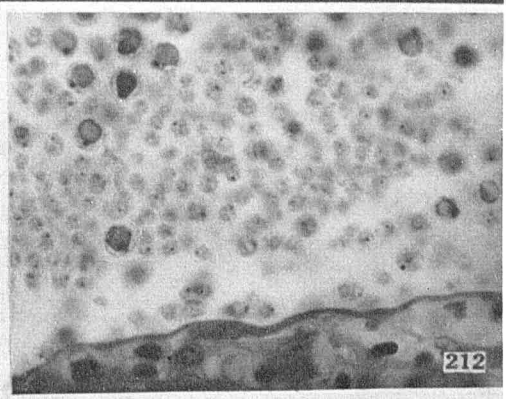
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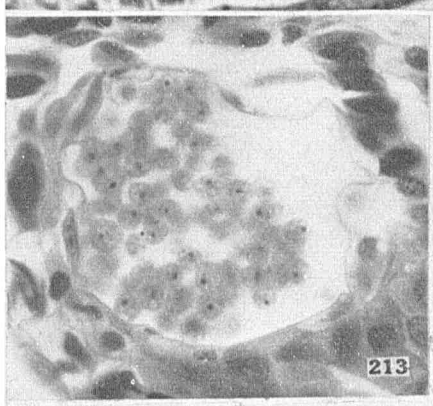
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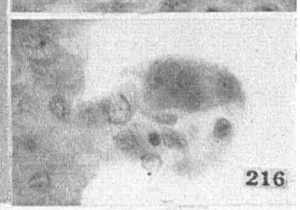
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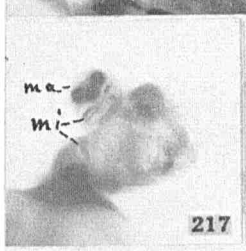
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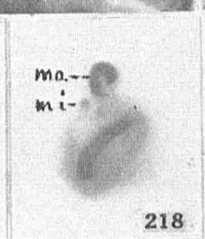
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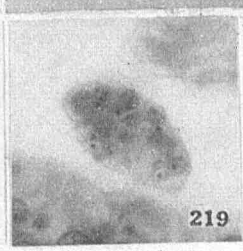
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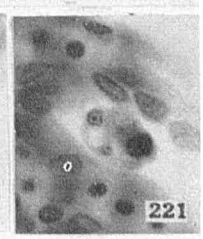
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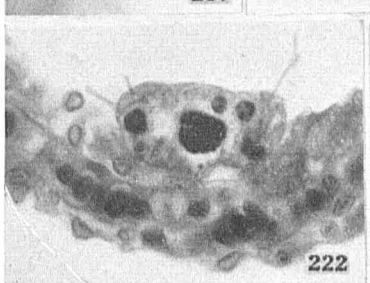
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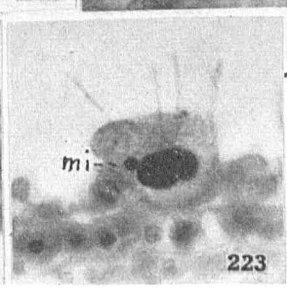
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UNITED STATES DEPARTMENT OF THE INTERIOR, J. A. KRUG, Secretary
FISH AND WILDLIFE SERVICE, ALBERT M. DAY, Director

EFFECT OF DIFFERENT CONCENTRATIONS OF MICRO-ORGANISMS ON THE FEEDING OF OYSTERS (*O. VIRGINICA*)

BY V. L. LOOSANOFF AND JAMES B. ENGLE

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ABSTRACT

These studies were conducted to learn what effect different concentrations of micro-organisms in sea water may have on the feeding activities of oysters. The micro-organisms were those which are considered as oyster food. Of these, *Chlorella* sp., *Nitzschia closterium* and *Euglena viridis* were most often used. It was found that heavy concentrations of micro-organisms interfered with the feeding of oysters by reducing the rate at which the oysters filtered the water through their gills. The type of shell movement was usually changed when the oysters were kept in water rich in micro-organisms. In very heavy concentrations pumping, and therefore feeding, ceased entirely. A correlation between the density of micro-organisms and the rate of feeding was often noticed. In light concentrations the rate of feeding and shell movements of the oysters remained normal and sometimes the presence of small quantities of plankton in sea water stimulated the pumping activities.

The size of the micro-organisms was found important because a much larger number of small cells, such as *Chlorella*, was needed to produce the same effect as caused by a smaller number of larger cells. Both the cells of the micro-organisms and the products which they released in the water affected the oysters. The cells interfered with the normal function of the gills, while the products which they released contained substances inhibiting the oysters.

The quantities of pseudo feces were usually roughly proportional to the quantities of food cells present in the water, whereas a reverse relationship existed in the formation of true feces. The presence of large quantities of pseudo feces usually indicated that feeding proceeded under the unfavorable condition caused by a heavy concentration of food cells in the water.

The results of the experiments showed that oysters feed efficiently only if the water contains small quantities of suspended matter. Oysters can also feed in water containing a relatively large number of micro-organisms, but under such conditions the rate of feeding is decreased.

EFFECT OF DIFFERENT CONCENTRATIONS OF MICRO-ORGANISMS ON THE FEEDING OF OYSTERS (*O. VIRGINICA*)[1]

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Since the middle of the last century, when cultivation of oysters became widely practiced in Europe and in this country, many interesting problems on the ecology and physiology of these mollusks have attracted the attention and efforts of biologists. The questions which from the very beginning aroused widespread interest were those dealing with the food and feeding of oysters. Numerous articles, discussions, and reviews of literature on these subjects have been since offered by many workers.[2]

Regardless of extensive studies there still remain several unsolved basic problems on the feeding of oysters. Of these, the one which deals with the relative efficiency of oysters feeding in clear or turbid water caused a strong controversy, but no conclusive evidence has been presented so far to uphold any of the theories advanced.[3] Also, in referring to turbidity of water it was not made clear whether it was due to the presence of rich plankton or to suspended particles of detritus and silt. Neither were any critical experiments made to determine whether there may be a correlation between the density of plankton population and the quantities of water pumped by the oysters. To clarify at least certain aspects of this complex problem we made a study of the effects of different concentration of micro-organisms upon the rate of pumping and, therefore, feeding of oysters and on the shell movements of these mollusks. While this will remain the chief theme, certain related problems will also be included in the scope of our discussion.

The oyster obtains its food by straining water through its gills and retaining the food particles, which are later directed toward the mouth. Thus, in addition to the respiratory and excretory functions the gills of the oysters also play a very important part in feeding. The complex structure and the functions of the oyster gills have been well described by a number of investigators.[4] An oyster can feed only if its shells are open and the entrance to the branchial cavity is not obstructed by the edges of the mantle. The rate at which the water passes through the oyster is controlled by the beat frequency of the lateral cilia of the gills, by the expansion and contraction of the gill ostia, the position of the edges of the mantle, and by the activity of the adductor muscle. The lateral cilia, which form rows along the filaments of the gills, propel the water into the passages of the gill lamellae. The water is then passed through the supra-branchial chambers and finally reaches the cloacal or promyal chamber from which it is dis-

[1] Approved for publication November 7, 1946. Fishery Bulletin 42.

[2] Martin 1923; Churchill and Lewis 1924; Savage 1925; Yonge 1926; Nelson 1938.

[3] Kellogg 1915; Grave 1916.

[4] Kellogg 1915; Yonge 1926; Nelson 1938.

NOTE.—We wish to express our thanks to Miss Frances Tommers and Messrs. William Arcisz and Charles Nomejko for their assistance during these studies and for analysis of the experimental data.

charged. The quantity of water leaving the oyster can be measured by the method described in this paper, thus the rate of pumping and, therefore, feeding can be easily estimated.

Biologists disagree about the effect of different quantities of material suspended in water upon the efficiency of feeding of oysters and related species. Kellogg (1915), after extensive studies of the arrangement and movements of the cilia of the gills, palps, and mantle cavities of a large number of lamellibranchs, concluded that these animals are able to feed only when the water is comparatively clear. He wrote, "It is my belief, after a good many years of observation, that lamellibranchs are able to feed only when the surrounding water is relatively free from solid particles; just how free, in a given case, I am not able to say, and the difficulties in determining the matter are great if not insurmountable." Kellogg concluded that the volume of food organisms and other particles suspended in the water determines whether the "collected foreign matter that reaches the palps shall proceed to the mouth or be removed from the palps." Grave (1916), on the other hand, disagreed with Kellogg's conclusions offering evidence that some food was found in the stomachs of oysters that were kept in very turbid water. Nelson (1921), Churchill and Lewis (1924), and later Yonge (1926) upheld Grave's opinion.

Yonge (1936) in his paper on the evolution of the swimming habits of lamellibranchs suggested that oysters evolved from ancestors that lived in very clear water and that the descent of some forms of lamellibranchs into more turbid waters was made possible by the evolutionary development of a more efficient cleansing mechanism involving not only the gills, palps, and mantle, but also the adductor and velum. He thinks that the possession of such efficient mechanisms made it possible for *O. virginica* and *O. angulata* to extend into muddier waters than *O. edulis*. Elsey (1935) found that *O. gigas* withstands existence in turbid water much better than *O. lurida*, which closely resembles *O. edulis*.

Dodgson (1928) working in England with *Mytilus edulis* also arrived at a conclusion directly opposite to that of Kellogg (1915). He maintained that mussels will feed and pass true feces when immersed in water so turbid that the animals are invisible at the depth of 2 to 3 inches. Fox, Sverdrup, and Cunningham (1937) in studying the rate of pumping by the California mussel, *M. californianus*, found that this animal also was capable of swallowing large amounts of calcareous mud from water containing a very heavy suspension of this material.

Churchill and Lewis (1924) studying very young fresh-water mussels, *Lampsilis luteola*, also noted that they could ingest particles of food and debris even when kept in very muddy water. These investigators think that mussels can and do feed when the water is heavily loaded with suspended material. More recently, however, Ellis (1936) showed that fresh-water mussels are at a distinct disadvantage if exposed to silt-laden waters. In his experiments, mussels retained in silt-free water kept their shells closed less than 50 percent of the time, while those in turbid water remained closed from 75 to 95 percent of the time.

The question of whether or not oysters and other lamellibranchs exercise selective power in ingesting plankton and small particles of detritus, or silt, is also a subject of controversy. Kellogg (1915) was one of the first to point out that these mollusks ingest small particles, regardless of their food value. Yonge (1923), Churchill and Lewis (1924), and Nelson (1924) expressed opinions which, in general, support Kellogg's contention. In the latter paper on this subject Yonge (1926) states that "Nothing but a purely mechanical or quantitative selection has been found in the oysters." In the same article Yonge says, however, that some lamellibranchs, such as *Syndosmya*, *Tellina*, or *Gari*, may exercise a certain qualitative selection of their food. Some protobranchs may do the same. Yonge points out, however, that in both cases such a qualitative selection, if occurring, takes place outside the mantle cavity.

The opposing theory, namely, that oysters and mussels possess the ability to select those particles which have definite food value, was advanced by Lotsy (1895), Allen (1914), and especially by Grave (1916), who maintained that oysters exercise a considerable choice in food material by reversing the direction of the beating of certain groups of cilia of the palps.

MATERIALS AND METHODS

The animal used in our work was the common American oyster, *Ostrea virginica*, of Long Island Sound. Only healthy individuals, varying from 4 to 6 years of age, were selected.

The micro-organisms, the effect of which we have studied, were (a) a green alga—*Chlorella* sp.; (b) a diatom—*Nitzschia closterium;* (c) a dinoflagellate—*Prorocentrum triangulatum;* and (d) a euglenoid—*Euglena viridis* (Loosanoff and Engle, 1942, 1944).[5] The forms selected were representative of four very large groups of organisms, which are regarded as constituting the bulk of the oyster food. Furthermore, each of the above-mentioned organisms had been considered by at least one author as playing an important part in the oyster diet. For example, Martin (1928) used *Chlorella* and *Nitzschia* in his experiments on the feeding of oysters, regarding them as very important sources of oyster food. He (Martin 1929) also found that *Prorocentrum triangulatum* is extremely common in Barnegat Bay, Delaware Bay, and Chesapeake Bay, where it is sometimes the most abundant organism in the stomach of the oyster. In still another article Martin (1927) stated that *Euglena* is digested by oysters.

The size of the forms used in our experiments varied from 5 microns (*Chlorella* sp.), to 60 microns (*Euglena viridis*). This difference helped to judge whether or not the size of the food organisms may have a certain effect, or effects, on the rate of pumping.

A method of cultivating micro-organisms, which we recently developed (Loosanoff and Engle 1942a), permitted us to grow the large quantities of plankton necessary for these studies. In some of our experiments as much as 100 gallons of culture were used daily. Because of the large quantities of food material needed it was impossible to keep the cultures quite bacteria-free, or even single-specied. Nevertheless, after some experience, we found it comparatively easy to grow mass cultures which were composed of practically one species.

We determined the number of organisms in the cultures with the Yoe photoelectric colorimeter. A detailed description of this apparatus and its uses was given by its designers[6] and, therefore, need not be repeated here. It will suffice to say that since in our determinations micro cells of 5.0 cc. capacity were used, the reading of the blank on the microammeter was set, as recommended by the designers, on the 25 mark instead of the 50.

[5] These forms were identified by Dr. James B. Lackey of the United States Public Health Service, to whom we wish to express our appreciation.

[6] Yoe and Crumpler 1935.

Before using the colorimeter in our experiments it was necessary to construct the curves for the conversion of the microammeter readings into the numbers of cells per cubic centimeter. We counted the number of cells per cc. of strong cultures and many of their dilutions using the Sedgwick-Rafter cell for *Nitzschia* and *Euglena*, and the Hellige haemocytometer for *Chlorella*. At least 10 counts were made for each dilution. Simultaneously with each count the reading was taken from the microammeter of the colorimeter. Finally, enough data were obtained to construct a curve by means of which the microammeter readings could be converted into the number of cells per cc. This method proved very rapid and accurate, extremely simplifying the work of determining the number of micro-organisms in the samples. Since our studies were largely confined to *Chlorella* sp., a curve used for the conversion of the microammeter readings into the numbers of *Chlorella* cells per cc. is given in figure 1.

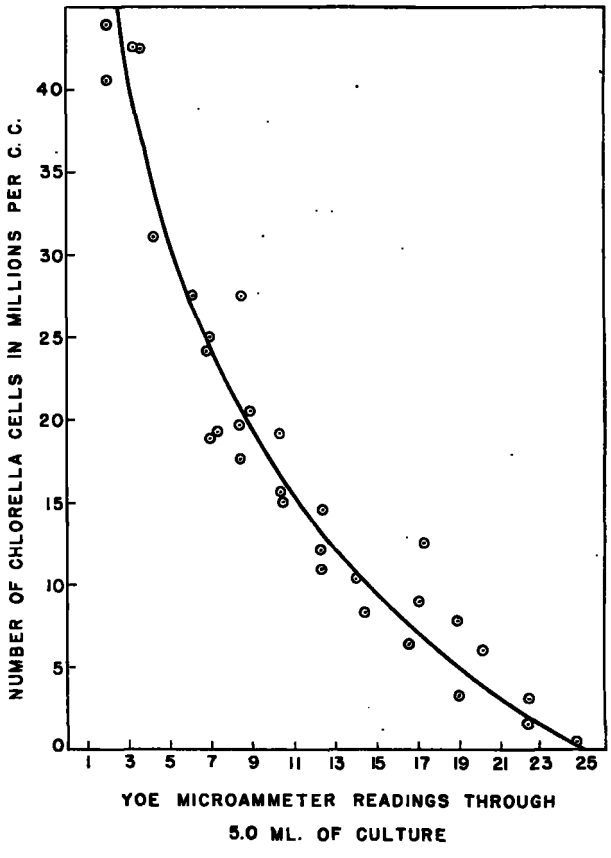

FIGURE 1.—Curve for the conversion of the microammeter readings into the number of *Chlorella* cells per cc.

Because only a few experiments were carried on with *P. triangulatum* no curve was constructed for this species. In using this form the relative density of the population of its cultures was determined with the colorimeter. Cultures, the microammeter readings of which were above 23, were considered as light, while those below that mark were regarded as medium and heavy.

As the success of our studies depended upon the employment of proper experimental methods, we give here a detailed description of the series of apparatus used. We do not claim credit for originality in devising all the apparatus, because several were made in accordance with well known mechanical principles, or represented modified and improved types of the models employed by other investigators. In some instances prototypes of apparatus have been used for many years. For example, the oyster chamber was first used by Galtsoff, while use of the apron was suggested by Moore (1908) and later employed by Nelson (1936). We would like to mention, however, that the series of apparatus, description of which we give, was used in our laboratory since 1937. Much of our apparatus, such as the constant-level chamber, which we devised, and the tripping vessel, which represents considerable improvement over the old types was made here and often loaned to other investigators working on problems, such as the reaction of oysters to chlorination and the various aspects of feeding of oysters.

The entire series of the apparatus is shown diagrammatically in figure 2. A group of six 15-gallon aquaria, *A*, connected with each other by

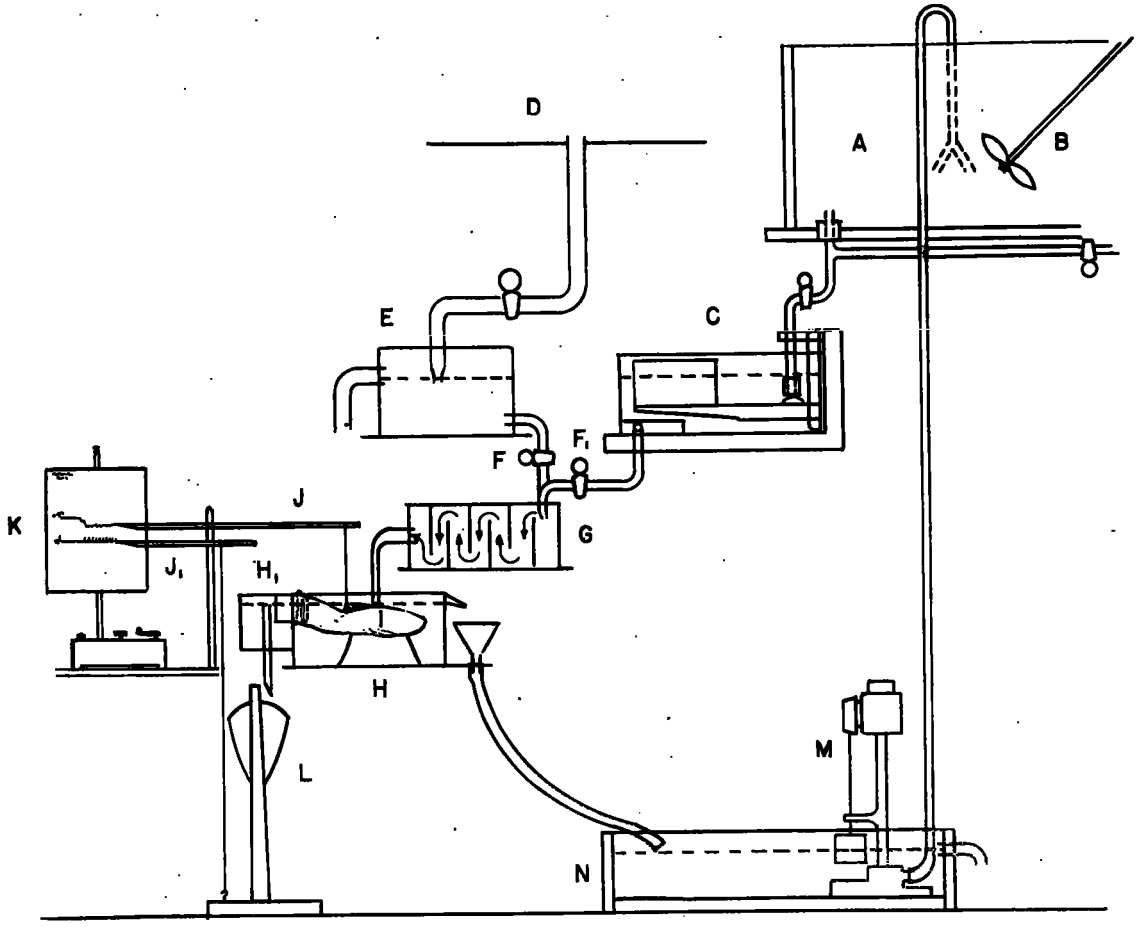

FIGURE 2.—Diagram of the series of apparatus employed to record the rate of water pumping and shell movements of the oyster. *A*—aquarium; *B*—stirrer; *C*—constant level unit; *D*—sea water storage tank; *E*—overflow chamber; *F* and F_1—flow adjusting valves; *G*—mixing trough; *H* and H_1—two compartments of the oyster chamber; *I*—oyster; *J*—lever recording shell movements of the oyster; J_1—lever recording movements of the tripping vessel *L*; *K*—kymograph; *L*—tripping vessel; *M*—pump; *N*—basin.

rubber tubes, was used as the reservoir for food cultures. By manipulating the clamps, or stop cocks, the aquaria could be used singly or in groups. When working with the organisms which had a tendency to settle on the bottom, the content of the aquaria was agitated by an electrical stirrer, *B*. Culture from the aquaria flowed into the constant-level unit, *C*, provided with an automatic float-control valve. This unit, which we devised, was so constructed that a steady level of liquid was constantly maintained within it. This device eliminated any waste of culture material, which would have occurred if a simple constant head overflow chamber had been used.

Sea water, pumped into a 5,000-gallon storage tank, *D*, located in the attic of the laboratory building, flowed into the overflow chamber, *E*, which was provided with an outlet, and thus also maintained a constant level. A uniform flow of culture or sea water, or any combination of the two, could be obtained by adjusting valves *F* and F_1. The fluids then entered the first compartment of the mixing trough, *G*, in which they were homogenized. We made the mixing trough in accordance with the principle commonly employed for the mixing and aeration of water flowing through the trough used in hatching salmon or trout eggs. The trough was divided into compartments by several dams which were so arranged as to cause the mixture to flow over the top of the first dam, then under the next dam, and again over the succeeding dam, repeating this process throughout the entire length of the trough. We found our trough much more satisfactory than other types, where stratification of liquids was often noted. The mixture finally entered the oyster chamber, *H*, containing the experimental oyster, *I*, the excurrent side of which was covered with a rubber cone-shaped apron that led the water pumped by the oyster into the smaller chamber, H_1. A silk string glued to the shell of the oyster, *I*, was attached to the counter balanced lever, *J*, which recorded every movement of the valve on the kymograph, *K*.

The water pumped by the oyster into chamber H_1, overflowed through the glass tube standpipe into the tripping vessel, *L*, of known capacity. When the vessel was filled with the water pumped by the oyster it tripped over, emptying its content, and at the same time striking a string attached to the lever, J_1, which touched the kymograph, *K*. Thus, each tripping was recorded, and because the capacity of the vessel was known, the quantity of water pumped by the oyster during certain intervals could be easily determined.

On rare occasions, when the quantity of culture was limited and it was necessary to save the overflow from the oyster chamber, *H*, an automatic sump pump, *M*, placed in a basin, *N*, designed to catch the overflow, returned the liquid to the culture reservoir, *A*.

Following is a more detailed description of some of the units that were briefly outlined above:

The constant level unit (*C* in fig. 2) is shown in detail in figure 3. The fluid from the culture reservoir flows through the intake tube, *A*, into the main chamber, *B*. As the level of the liquid in the

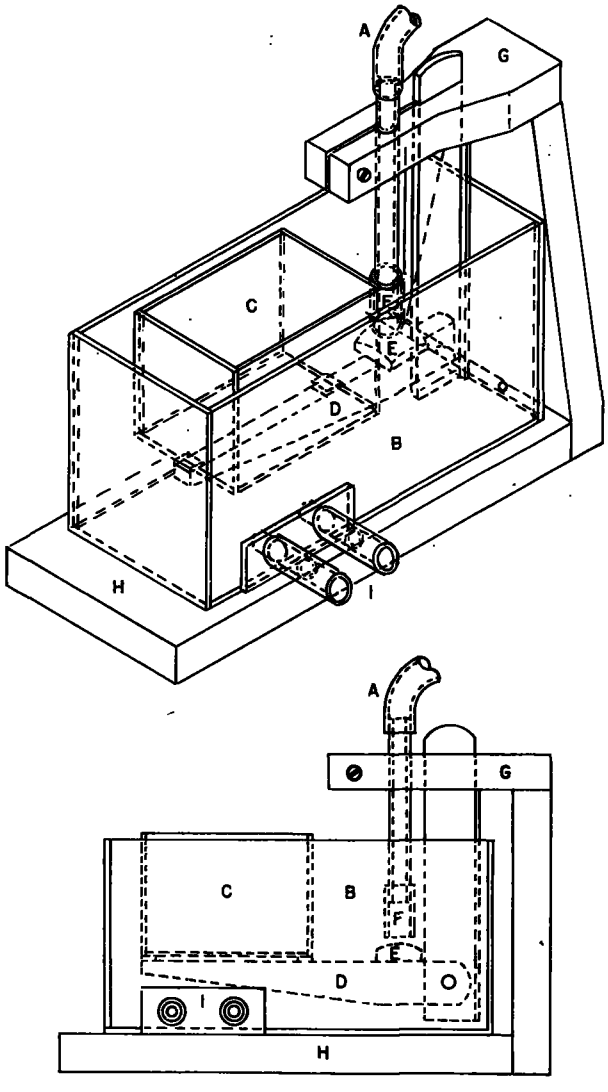

FIGURE 3.—Constant-level chamber. Description in text.

chamber rises, the float, *C*, attached to the hinged lever, *D*, also rises and finally, when a certain level is reached, pulls the valve seat, *E*, tightly against the rubber valve, *F*, which is then closed and the flow of liquid stopped. The position of the valve is adjustable by moving the intake tube up or down and by holding it in the desired position by a clamp, *G*, which is part of the base that holds the whole unit. The liquid is drawn from the chamber through the outlet tubes, *I*, to the mixing trough (*G* in fig. 2).

The details of the oyster chamber are shown in figure 4. The fluid from the mixing trough flows

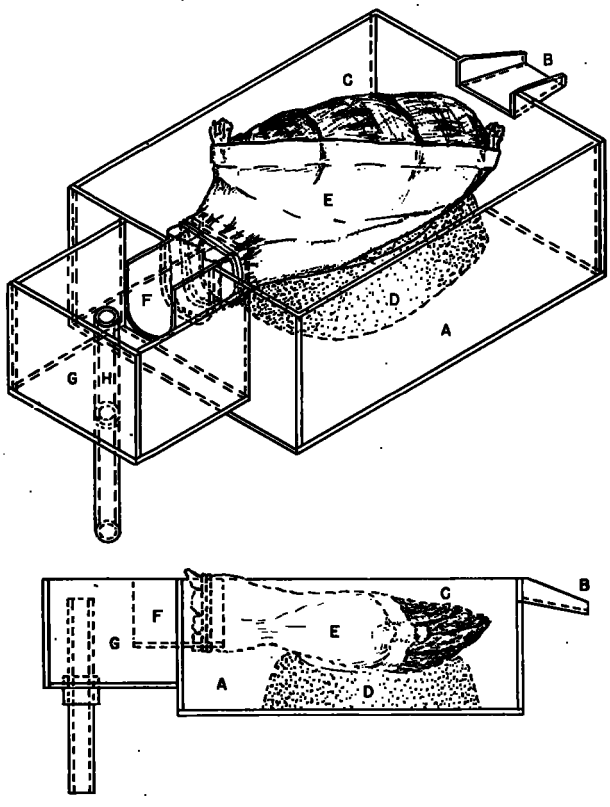

FIGURE 4.—Oyster chamber. Description in text.

into the oyster chamber, *A*. The excess of fluid not utilized by the oyster leaves the chamber through the opening, *B*. The oyster, *C*, lying with its flat valve uppermost on the concrete base, *D*, has its excurrent side enclosed in a rubber cone or apron, *E*, that is tightly attached to the trough, *F*, which leads the water pumped by the oyster into the overflow chamber, *G*. A standpipe, *H*, is adjusted in height to a level slightly above that of level, *B*, of the oyster chamber. The proper adjustment of the height of the standpipe is very important to prevent a syphoning effect from the oyster chamber to the overflow chamber. The sensitivity of the standpipe must be such that a few drops of water added to the chamber, *G*, will immediately start an overflow through the pipe.

In measuring the rate of water flow the correct results depended upon the principle that the flow of water between the oyster chamber, *A*, and the overflow chamber, *G*, could take place only through the interior of the oyster and be caused only by the pumping activities of the animal. Therefore, we took every precaution to avoid leakage of water from one chamber to the other by properly attaching the apron, *E*, to the trough, *F*, and to the oyster. The water-tight connection between the apron and the trough was easily made by using a heavy rubber band, which presses the apron to the sides of the funnel connecting the two chambers. Attachment of the apron to the oyster was, however, more complicated and, therefore, requires a more detailed description. We offer the steps of this operation below:

1. The surface of the shell was scrubbed clean.
2. When dry the shell was washed with alcohol, and again allowed to dry. Care was taken to keep the alcohol from entering the interior of the oyster.
3. A layer of liquid rubber cement was spread on the shell along the line where the apron was to be attached. This line extended around the long axis of the oyster.
4. A strip of one-half-inch rubber tape was pressed firmly against the shell along the line of the applied rubber cement, except at the points where the tape made the turns around the hinge and bill of the oyster.
5. Cotton plugs were inserted between the bill of the oystershell and the tape, and between the hinge and the tape. This arrangement allowed for freedom of shell movement and yet maintained a leak-proof joint.
6. When the rubber tape was glued tightly to the shell a layer of rubber cement was put on its upper surface. Then a piece of dental-rubber dam, cut long enough to fit completely around the oyster with a little overlapping for joining the ends to form the cone, was glued to the rubber tape. The rubber cone covered only the excurrent part of the oyster, while the incurrent side was left free. The small end of the rubber cone was attached and by a rubber band was held tightly to the trough connecting the oyster and the overflow chambers.

Our type of tripping vessel (*L* in fig. 2) is shown in figure 5. The liquid from the overflow chamber (*G* in fig. 4) is led by the standpipe (*H* in fig. 4) to flow into the main receptacle, *A*, of the tripping vessel. As the liquid rises, a float, *B*, also rises until the arm, *C*, clears the notch in the side of the main receptacle and the top-heavy vessel trips over spilling out its water content. The vessel is returned to the normal upright position by the pull of the counter weight, *D*. As the vessel goes through the partial revolution which empties it, the silk string, *E*, is touched thus making a mark on the kymograph record. The vessel is suspended over the base, *G*, by two adjusting screws, *F*.

The sea water overflow chamber is of relatively simple construction (fig. 6). The water flows in the chamber, *B*, through the spigot, *A*, and is fed to the experimental animals through the outlets, *D*. The excess water overflows through the pipe, *C*.

We made all the apparatus from sheets of cellulose acetate, commonly known as plastocoele. The shavings of this material dissolved in acetone served as glue.

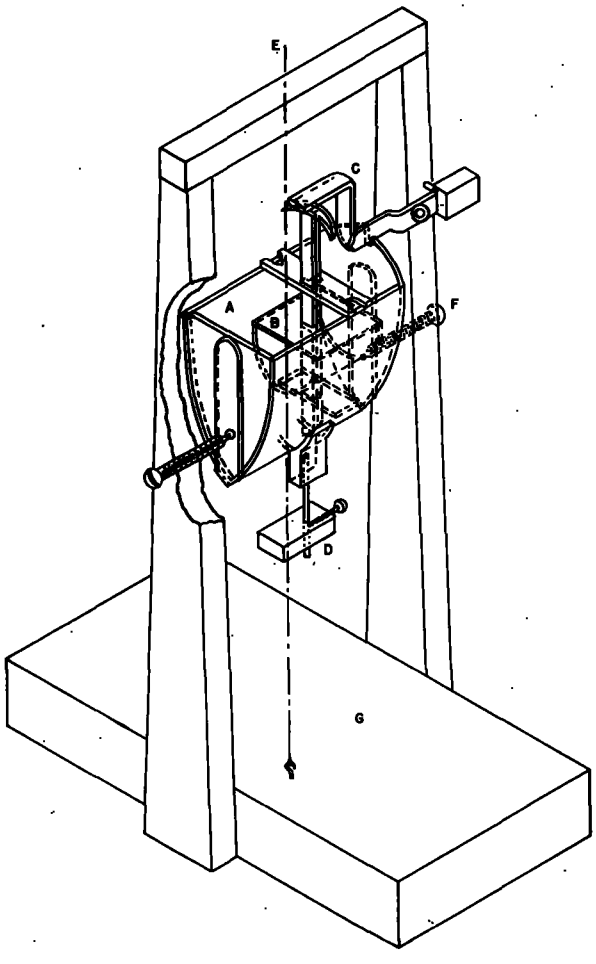

FIGURE 5.—Tripping vessel. Description in text.

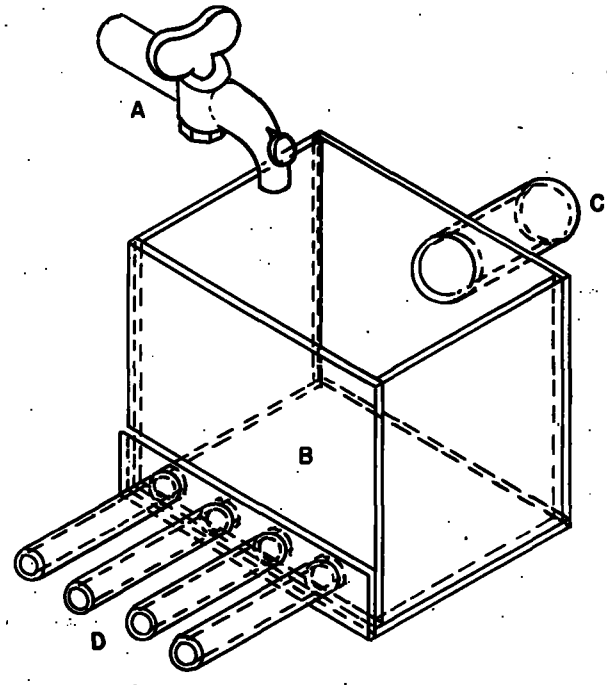

FIGURE 6.—Sea-water overflow chamber. Description in text.

The kymograph drums usually rotated at the rate of 1¼ inches per hour. When necessary, an interval timing device was also connected to the kymograph. The records obtained provided information regarding the shell movement of the oysters and the rate at which the animals pumped the water. A section of such a record is given in figure 7.

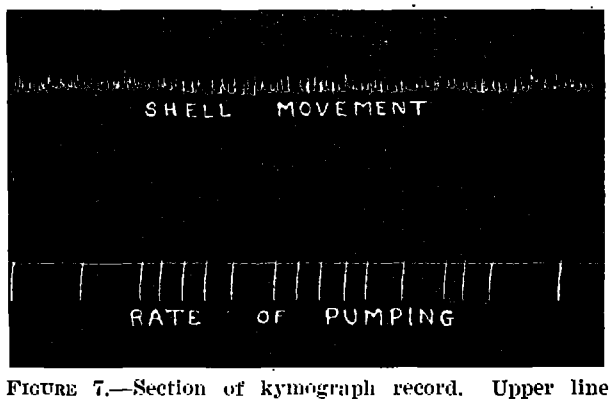

FIGURE 7.—Section of kymograph record. Upper line shows the shell movements of the oyster, and the lower indicates the rate of pumping. Each vertical line of the lower record designates the emptying of the tripping vessel of 239 cc. capacity.

EXPERIMENTS AND OBSERVATIONS

PRELIMINARY EXPERIMENTS

At the beginning of this work it was our opinion that oysters kept under favorable conditions would "fatten" if given large quantities of food. Accordingly, we placed oysters in large, outdoor, tide-filled tanks to which rich, mixed cultures of micro-organisms were added. Regardless of such presumably favorable conditions, the oysters failed to show improvement and usually became poorer than the control animal kept in the tank with ordinary sea water. Sometimes, when very large quantities of food organisms were added to the water, the oysters became sick and many died. Examination showed that the stomachs of the oysters that were still alive were empty and that the crystalline style was absent.

At first we could not suggest the direct cause of the poor condition of the oysters but, as our studies progressed, we began to suspect that large quantities of micro-organisms in the water were interfering with the normal feeding behavior of the mollusks. To verify this suspicion we made a preliminary series of experiments to determine the effect of micro-organisms of various types and in different concentrations upon the oysters.

In all our experiments we kept the salinity and temperature of the cultures equal to or closely approaching those of sea water. In some cases it was also found necessary to control the pH of the cultures. This was easily accomplished by regulating the intensity of the light striking the glass walls of the aquaria containing the cultures. By placing the culture in direct sunlight its pH would be quickly increased, whereas by shading the aquaria the pH could be reduced. As a rule, however, the pH of the cultures ranged from 7.8 to 8.2, thus closely resembling that of the sea water used in the experiments.

In the first, rather exploratory series of experiments, we exposed the oysters for periods ranging from 20 to 52 hours to a constant flow of sea water containing *Chlorella* cells in different concentrations. Before that, however, we kept the oysters for at least 12 hours in running sea water to obtain a record of their activities under normal conditions. The change from ordinary sea water to that containing the cultures was always accomplished by simultaneously shutting off the flow of one and turning on the other. Thus the change was accomplished without disturbing the experimental oysters.

The numbers of the *Chlorella* to which the oysters were subjected ranged from about 1½ to 5½ million cells per cc. of sea water. We noticed that in the concentrations of approximately 2.0 million cells per cc. and heavier the oysters became affected (fig. 8). The rate of pumping, i. e., feeding

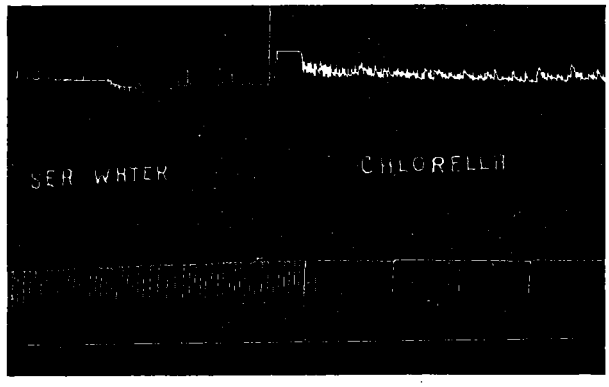

FIGURE 8.—Changes in shell movements and in the rate of pumping of the oyster when ordinary sea water was substituted with that containing approximately 5 million *Chlorella* cells per cc. Each vertical line of the lower record represents 244 cc. of water pumped by the oyster.

markedly decreased, as compared with the rate of pumping of the same oysters before they were exposed to *Chlorella*. This decrease varied from 69 to 90 percent in concentrations of about 5½ million cells per cc., and in somewhat lighter concentrations, between 2 and 3 million cells per cc., it ranged from 19 to 56 percent.

The kymograph records of the shell movements of the oysters showed that exposure to a concentration of 5½ million cells of *Chlorella* per cc. did not decrease the time the oysters kept their shells open. They indicated, nevertheless, that the type of shell movement during the exposure noticeably differed from that observed while the oysters were kept in running sea water (fig. 8).

During the periods when the oysters exposed to the concentrations of *Chlorella* showed a decrease in the rate of flow and a change in the type of shell movement, the control oysters kept in running sea water functioned normally.

After observing that the strong concentrations of *Chlorella* depressed the feeding activities of the oysters and changed the character of their shell movements we decided to determine whether com-

paratively light concentrations would have the same effect. We subjected 10 oysters first to a flow of sea water and then to a weak culture of *Chlorella* of approximately 500,000 cells per cc. We found that in about half the cases the rate of pumping somewhat increased when the oysters were kept in weak *Chlorella* culture, but in the others a slight decrease was seen. Some oysters showed no appreciable change in the rate of pumping when sea water was substituted with a weak *Chlorella* culture (fig. 9). The change from one condition to another did not change the type of the shell movements of the oysters. The behavior of the control oysters was not basically different from that of the experimental ones. Therefore, we concluded that light concentrations of *Chlorella*, such as 500,000 cells per cc., did not affect the oysters unfavorably.

FIGURE 9.—Kymograph record showing that no appreciable change in the shell movements and the rate of pumping of the oyster occurred when the flow of sea water was substituted with that of weak *Chlorella* of 500,000 cells per cc. Each vertical line of the lower record represents the emptying of the tripping vessel of 265 cc. capacity.

Practically the same results were obtained when the oysters were exposed to light concentrations of *Nitzschia* of 20 to 30 thousand cells per cc., and to *Prorocentrum triangulatum*.

EXPOSURE OF OYSTERS TO INCREASING AND DECREASING CONCENTRATIONS OF MICRO-ORGANISMS

In the next series of experiments we subjected the oysters to gradually increasing concentrations of *Chlorella*. As usual, to obtain a record of the normal behavior of the oysters they were first exposed to a flow of sea water. The average quantity of water pumped hourly by each oyster during that period was found and accepted as normal, or 100 percent. Any deviations in the rate of pumping in subsequent exposures were estimated in relation to that figure. After the exposure to sea water the oysters were subjected for hourly periods to increasing concentrations of *Chlorella* ranging from approximately 2 to 13 million cells per cc. (fig. 10). The different concentrations were

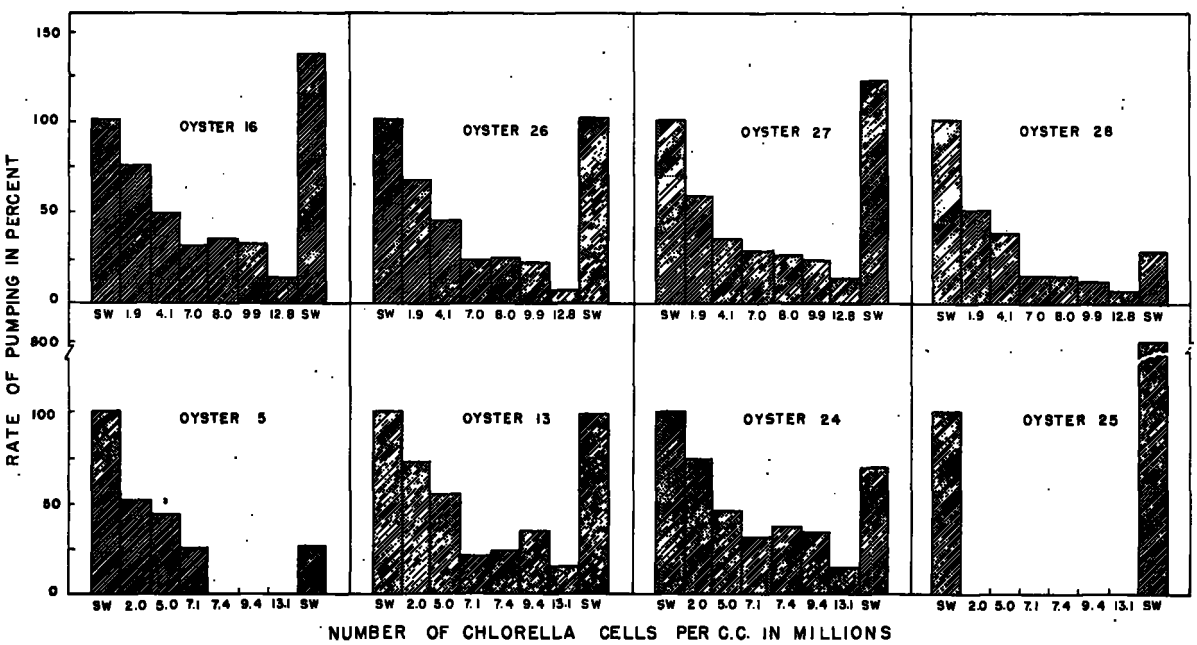

FIGURE 10.—Histogram showing rate of pumping (percentage) of eight oysters exposed to increasing concentrations of *Chlorella*. Rate of pumping in sea water (SW) at the beginning of the experiment was taken as 100 percent.

made by diluting the original heavy culture with the needed quantities of sea water.

Upon the change from ordinary sea water to that containing about 2 million cells of *Chlorella* per cc. the rate of pumping of the oysters sharply declined. Some oysters, as oyster No. 25, ceased to pump entirely, although the shells remained open (table 1) and moving (fig. 10). In other oysters the rate of pumping was reduced from 52 to 76 percent of the original rate.

Subsequent increases in the density of the *Chlorella* resulted in further decreases in the rate of pumping. In general, the decrease became more pronounced as the concentration of the cells increased. In the heaviest concentration, which was approximately 13 million cells per cc., several oysters, although open, did not pump any water. In other oysters the rate of pumping was only from 8 to 21 percent of that recorded in sea water, before the oysters were subjected to water containing *Chlorella*.

TABLE 1.—*Percentage of time oysters remained open when subjected to increasing concentrations of Chlorella*

Number of cells per cc.	Temperature ° C.	Percentage of time open			
		Oyster number			
		16	26	27	28
Sea water	22.0	100	100	100	100
1,900,000	21.4	100	100	100	100
4,125,000	21.2	100	100	100	100
7,000,000	21.2	100	100	100	100
8,000,000	21.0	100	100	100	100
9,875,000	20.0	100	100	100	100
12,750,000	20.0	100	39	75	75
Sea water	20.5	100	100	100	100
		Oyster number			
		24	5	25	13
Sea water	22.0	100	100	100	100
2,000,000	22.0	100	100	92	100
5,000,000	21.8	100	100	58	100
7,125,000	22.0	100	78	17	58
7,375,000	21.8	100	0	75	58
9,375,000	21.6	100	0	0	100
13,125,000	21.0	77	15	0	64
Sea water	21.3	100	100	100	100

When at the end of the exposure to *Chlorella* the oysters were again in sea water their rate of pumping usually showed a marked increase (figs. 10 and 11). Often they pumped more vigorously than during the period at the beginning of the experiment when their normal rate of pumping was ascertained. Such intensive pumping suggested that the oysters tried to cleanse themselves of the cells which accumulated in the gills and

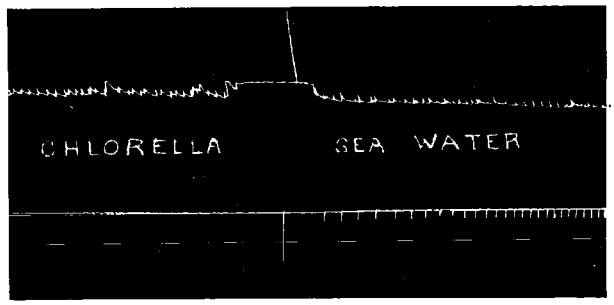

FIGURE 11.—Section of the kymograph record showing the resumption of rapid pumping by the oyster when heavy *Chlorella* culture of approximately 13 million cells per cc. of sea water was substituted. Note that while in the *Chlorella* culture the shells of the oyster were moving although no water was being pumped. Each vertical line of the lower record represents 246 cc. of water pumped by the oyster.

mantle chamber. The cleansing action, as shown by very fast pumping, became evident almost immediately after the oysters were returned to sea water, but reached its maximum intensity somewhat later.

Exposing the oysters to increasing concentrations of *Chlorella* did not immediately change the percentage of time the shells remained open (table 1). However, as the concentrations were increased, the shells of several oysters were closed for some time, and in the heaviest concentration the time the shells remained open was reduced in almost every case. Nevertheless, no definite correlation was found between the increase in the number of *Chlorella* cells and the time the oyster shells remained open.

In the next series of experiments the process of exposure of the oysters to different concentrations of *Chlorella* was reversed. The oysters, after having been kept in sea water for several hours, were subjected to decreasing concentrations of the strength indicated in figure 12 and table 2. They were kept in each concentration for a period of 1 hour.

The first concentration, used immediately after the sea water, was very heavy, containing approximately 16 million cells per cc. (fig. 12 and table 2). The contact of the oysters with such a heavy cell population always resulted in a rapid and marked decrease in the rate of pumping. Some oysters ceased pumping entirely, as if they were unable to cope with the mass of cells present in the surrounding water (fig. 13). Apparently the initial

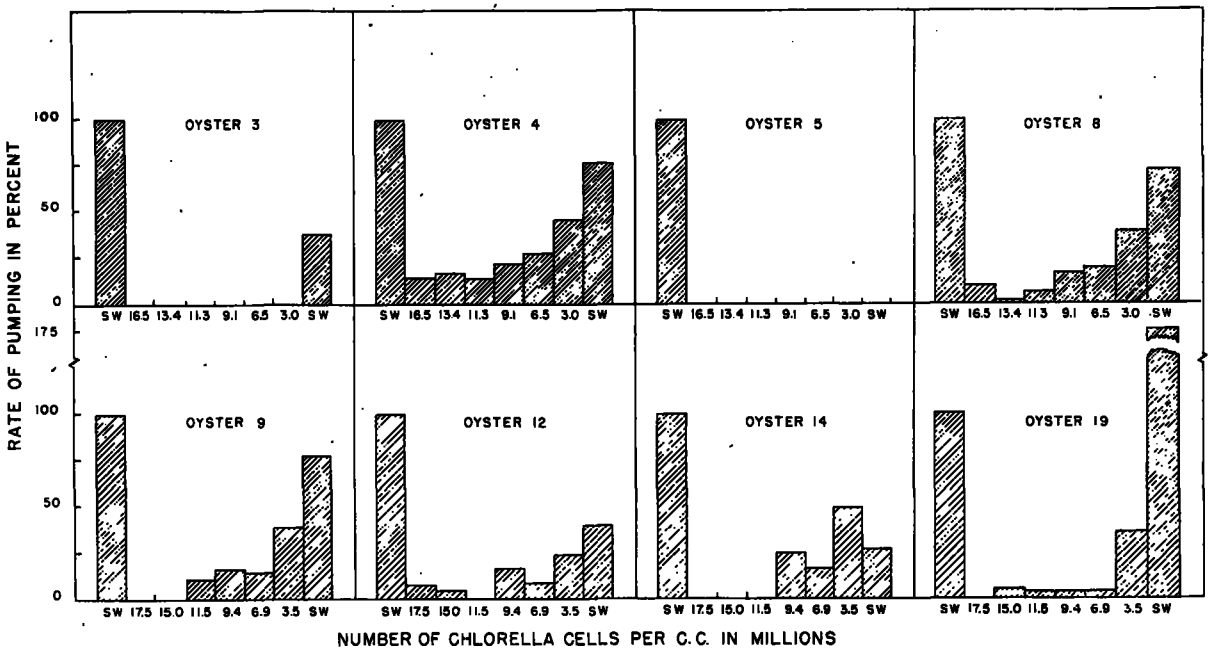

FIGURE 12.—Histogram showing rate of pumping (percentage) of eight oysters exposed to decreasing concentrations of *Chlorella*. Rate of pumping in sea water (SW) at the beginning of the experiment was taken as 100 percent.

shock received by the oysters had a lasting effect, because many of them kept their shells closed, or were open but not pumping any water for several hours, although, meanwhile, the concentrations of *Chlorella* were gradually reduced (fig. 12).

Some oysters, the pumping activities of which were stopped by the initial strong concentration, later showed an increase in the rate of pumping, which roughly corresponded to the decrease in the number of *Chlorella* cells (fig. 12, oysters Nos. 4, 8, and 9). The increase was especially noticeable in the weakest concentration tried, which was approximately 3 million cells per cc. However, the quantities of water pumped during that period were much smaller than those recorded at the beginning of the experiment when the oysters were kept in sea water.

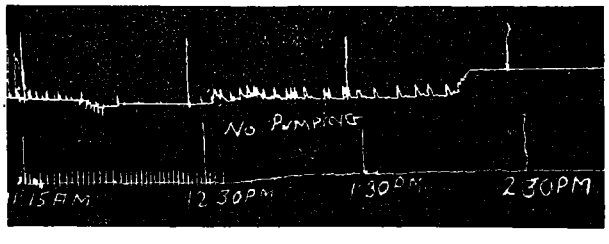

FIGURE 13.—Section of the kymograph record showing cessation of pumping and the change in the type of shell movements of the oyster when sea water was substituted at 12:30 p. m. with a flow of *Chlorella* culture containing approximately 16 million cells per cc. Each short vertical line of the lower record represents 259 cc. of water pumped by the oyster.

Following the weakest concentration of *Chlorella*, sea water was again flowed into the chambers

TABLE 2.—*Percentage of time oysters remained open when subjected to decreasing concentrations of Chlorella*

Number of cells per cc.	Temperature ° C.	Percentage of time open			
		Oyster number			
		3	4	5	8
Sea water	22.9	100	100	100	100
16,500,000	22.7	100	100	67	100
13,375,000	20.2	75	100	0	17
11,250,000	20.9	0	100	33	75
9,125,000	22.1	0	100	0	100
6,500,000	----------	0	100	0	100
3,000,000	22.3	0	100	0	100
Sea water	22.9	100	100	100	92
		Oyster number			
		9	12	14	19
Sea water	21.2	100	92	83	75
17,500,000	18.8	0	79	0	0
15,000,000	18.7	0	8	0	13
11,500,000	19.7	9	0	0	100
9,375,000	20.4	100	42	67	100
6,875,000	20.9	100	100	60	100
3,500,000	----------	100	100	97	100
Sea water	21.9	100	100	50	100

containing the oysters. As soon as the water replaced the culture, the oysters resumed a rapid rate of pumping. However, in the majority of oysters the rate of pumping, although rather rapid, did not equal or exceed that recorded in sea water at the beginning of the experiment (fig. 12). We ascribed this to a prolonged exposure to dense concentrations of *Chlorella* which probably temporarily affected the pumping mechanism of the oysters.

Our observations on the shell movements of oysters in these experiments, as well as in many other studies of a similar nature which we will describe later in this article, showed two facts of considerable significance. First, we noted that sometimes the shells remained open for long periods, often lasting several hours (table 2), although the oysters did not pump any water (fig. 13). These observations showed conclusively that, although the shells of the oysters may be open, this fact cannot be always interpreted that the oysters are actively feeding. Hopkins (1933) working with *Ostrea gigas* was the first to observe that sometimes, when the shells of the oysters are wide open, no flow of water is produced. He found that in most of such instances the entrance to the branchial cavity is completely closed by the borders of the mantle. Under such a condition the animals are incapable of pumping water and, therefore, feeding.

Our second observation concerned the change in character of the shell movements of the oysters after sea water was substituted with *Chlorella*. We noted that the shell movements usually became of greater amplitude and of a type different than that observed in the same individuals under normal conditions (fig. 13). Our numerous records showed that this type of shell movement was always made when the oysters were kept in heavily laden water and were ejecting large quantities of pseudo feces at frequent intervals. Incidentally, this type of shell movement closely resembles that shown by Nelson (1921) in his figure 3, which he interprets as the type indicating active feeding of oysters. Actually, as is seen on the kymograph record shown in our figure 13, the rate of feeding of oysters may be markedly reduced or even entirely stopped when the shell movements are of this type.

Experiments in which we used *Nitzschia closterium* fully substantiated and corroborated all general conclusions formed during the studies of effects of *Chlorella* upon the rate of pumping and character of the shell movements of oysters. We found that the concentrations of *Nitzschia* of less than 70 to 80 thousand cells per cc. usually did not adversely affect the activities of the oysters (fig. 14). Heavier concentrations, however, not only

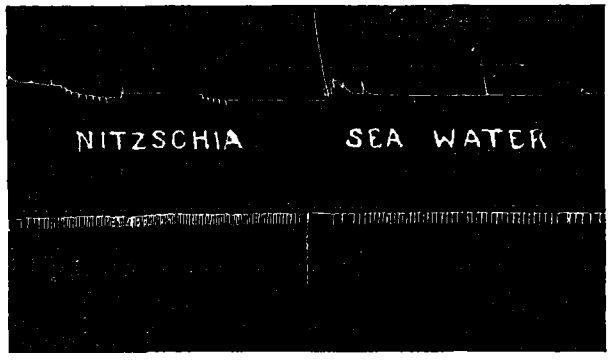

FIGURE 14.—Section of the kymograph record showing that a light concentration of *Nitzschia* of approximately 30,000 cells per cc. did not depress the pumping rate of the oyster. In this case the rate of pumping in *Nitzschia* was somewhat greater than in sea water. Each vertical line of the lower record represents 246 cc. of water pumped by the oyster.

reduced the rate of flow but also affected the character of the shell movements (fig. 15). Data of the same nature were obtained when *Prorocentrum* cultures were used (fig. 16).

EXPERIMENTS WITH *EUGLENA VIRIDIS*

We devoted the next series of experiments to studies of the behavior of oysters in different con-

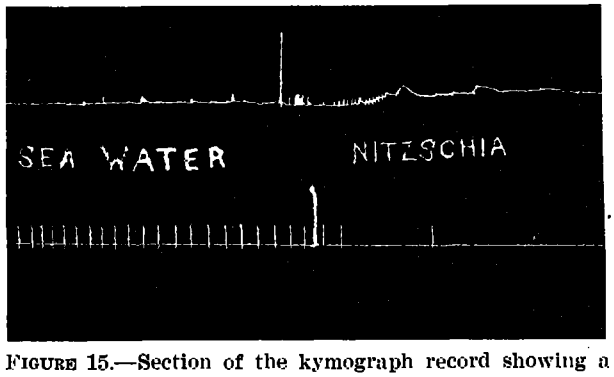

FIGURE 15.—Section of the kymograph record showing a very prominent reduction in the rate of pumping, and a change in the type of shell movements of the oyster subjected to a heavy concentration of *Nitzschia* of approximately 200,000 cells per cc. Each vertical line of the lower record represents 310 cc. of water pumped by the oyster.

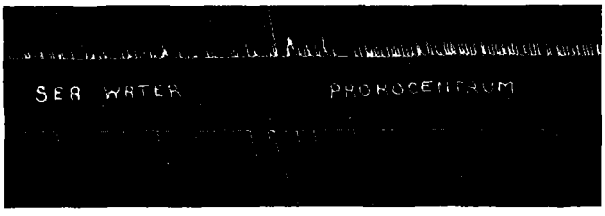

FIGURE 16.—Section of the kymograph record showing a very prominent reduction in the rate of pumping, and a change in the type of shell movement of the oyster subjected to a heavy concentration of *Prorocentrum*. Each vertical line of the lower record represents 267 cc. of water pumped by the oyster.

centrations of *Euglena viridis*, a form which is of a considerably larger size than any of the three microorganisms tried before. *Euglena* was easily cultivated but in working with it certain precautions were necessary to maintain the cells uniformly distributed in the water. Because of their relatively large size the euglenoids did not easily remain in suspension, as was the case with *Chlorella*, *Prorocentrum*, and *Nitzschia*, but quickly settled on the bottom. Also, they were negatively phototropic, showing a constant tendency to move away from the side of the aquarium receiving the most light. We easily overcame these difficulties by a strong agitation of the aquarium content and by regulation of the light.

The organism was identified for us by Dr. James B. Lackey, chief biologist of the United States Public Health Service who in his letter to the senior author said: "This I would call an absolutely typical *Euglena viridis*. However, this species has never been reported, to the best of my knowledge, from salt water and judging from other organisms in your sample it was evidently salt water which you sent me. If you have acclimated this species it is an interesting biological accomplishment." In our work this species was easily cultivated in the outdoor tanks placed under a roof and in the laboratory aquaria kept away from direct sunlight. The salinity of the water in which the cultures were raised was usually about 27 parts per thousand. However, in some aquaria *Euglena* lived well even when the salinity was 32 parts per thousand.

As in the previous experiments, our first observations consisted in determining the effects of very light concentrations of the cells upon the oysters. The first concentrations tried contained only about 1 or 2 thousand *Euglena* per cc. of water. These concentrations did not disturb the oysters. In several instances the rate of pumping even showed a considerable increase. The type of the shell movements remained the same as that recorded before the flow of sea water was substituted with a weak concentration of *Euglena*.

Somewhat stronger concentrations, ranging from 3 to 5 thousand cells per cc., began to affect the oysters (fig. 17). Usually, as soon as the oysters came in contact with these concentrations, the pumping decreased and the type of shell movements changed. The change was often accompanied by the formation of large quantities of pseudo feces. However, some cases were also recorded where the animals exposed to such concentrations remained apparently undisturbed or even pumped larger quantities of water.

In heavier concentrations, containing approximately 8,000 or more cells of *Euglena* per cc. of water, the oysters were obviously under unfavorable conditions because the rate of pumping was sharply reduced and the type of shell movements changed (fig. 18). Many oysters kept their shells open and moving, but did not pump water. We also noted that after being changed from a heavy culture of *Euglena* to sea water the oysters began to pump water very rapidly as if to cleanse their gills (fig. 19). It may be recalled that we made similar observations when forms other than *Euglena* were used.

To demonstrate the rapid changes in the rate of pumping and in the type of shell movements shown of the oysters when they are changed from sea water to *Euglena* culture, and vice versa, we made a supplementary series of experiments. It consisted in subjecting oysters intermittently for

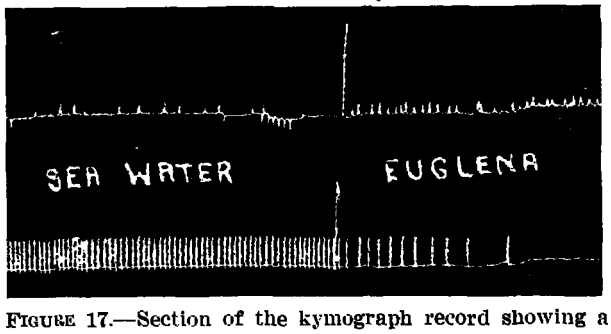

FIGURE 17.—Section of the kymograph record showing a reduction in the rate of pumping, and a change in the type of shell movements of the oyster subjected to a *Euglena* concentration of approximately 5,000 cells per cc. Each vertical line of the lower record represents 265 cc. of water pumped by the oyster.

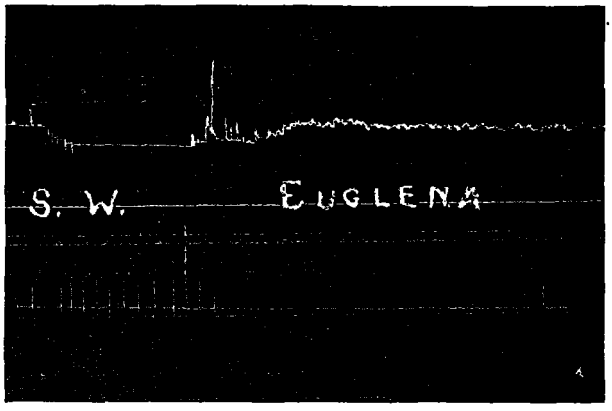

FIGURE 18.—Section of the kymograph record showing a drastic reduction in the rate of pumping, and a change in the shell movements of the oyster subjected to a culture of *Euglena* of approximately 12,000 cells per cc. Each vertical line of the lower record represents 267 cc. of water pumped by the oyster.

periods of 2 hours to a flow of sea water and to *Euglena* culture. Four experiments, each employing four oysters, were made. In the first one 3,300 cells of *Euglena* per cc. of sea water were used and in the following ones we employed concentrations of 8,000, 11,300, and 25,000 cells per cc. Care was taken to keep the temperature, salinity, and hydrogen-ion concentration of the ordinary sea water and of that containing *Euglena* alike, or nearly alike. For the entire series the temperature was about 21.0° C. and the salinity, approximately 27.0 parts per thousand. The pH of both the sea water and the culture varied between 7.8 and 8.2.

Even while the lightest concentration was tried the difference in the behavior of the oysters in sea water and in *Euglena* culture cells was noted, although it was not always sharply defined. In the stronger concentrations of 8,000 and 11,300 cells

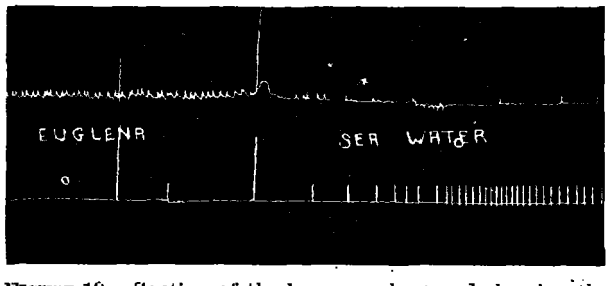

FIGURE 19.—Section of the kymograph record showing the changes in the rate of pumping and shell movements of the oyster after a flow of strong *Euglena* culture of approximately 12,000 cells per cc. was substituted with sea water. Each short vertical line of the lower record represents 265 cc. of water pumped by the oyster.

per cc. the difference became clear. Usually, the rate of pumping decreased upon the change from sea water to *Euglena*, and increased when the oysters were again exposed to sea water. Sometimes, during the periods when the oysters were exposed to *Euglena*, pumping was entirely discontinued, although the shells of the experimental animals remained open and moved, vigorously expelling a large mass of pseudo feces.

The strongest concentration of *Euglena* which we used in this series of experiments contained 25,000 cells per cc. (fig. 20). Always, when the

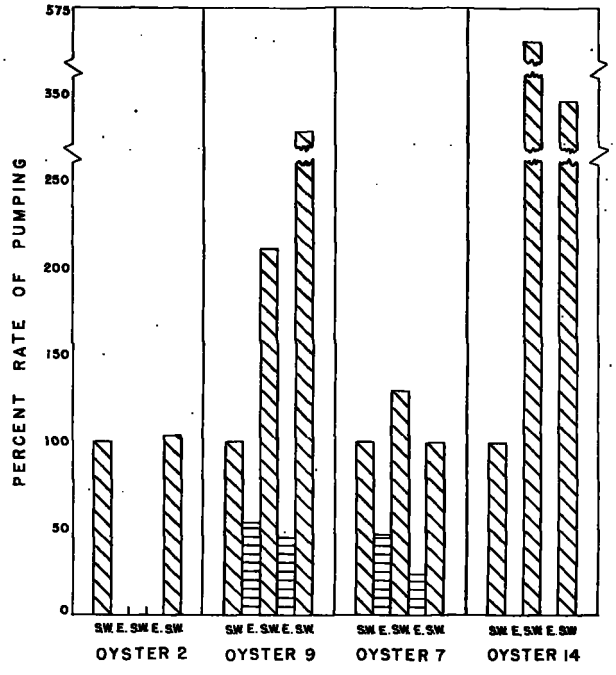

FIGURE 20.—Diagram showing percentage rate of pumping of four oysters subjected intermittently for periods of 2 hours to sea water (SW) and to *Euglena* culture (E) containing approximately 25,000 cells per cc. Rate of pumping in sea water prior to the first exposure to *Euglena* was taken as 100 percent.

oysters were open, the change from sea water to *Euglena* culture resulted in a decrease in the rate of pumping. Oyster No. 2 closed after the flow of the culture was substituted for sea water and remained closed for 6 hours. Three other oysters, however, had their shells open. While exposed to *Euglena*, oyster No. 14 was wide open and moved its shells vigorously, although pumping ceased. Usually the change from *Euglena* culture to sea water resulted in the resumption of pumping, and

the rate of flow often exceeded that of the initial period.

The final series of observations in which we used *Euglena viridis* consisted in subjecting the oysters to increasing concentrations of this form (fig. 21). Two separate experiments, each with four oysters, were run. In the first one the oysters, after their rate of pumping in sea water had been determined, were subjected for hourly periods to various dilutions of strong *Euglena* culture ranging from 8,600 to 63,000 cells per cc. In the second experiment the number of cells ranged from 12,600 to 94,600 per cc. As a rule, the change from sea water to *Euglena* culture always resulted in a considerable decrease in the rate of pumping. A further increase in the density of the *Euglena* population showed even greater interference with the pumping activites of the oysters. Some oysters, such as No. 31, had their shells open for several hours while exposed to dense concentrations of *Euglena*, but did not pump water. With the exception of oyster No. 40, which remained closed for several hours, and oyster No. 38, which closed its shells while exposed to concentrations of 54,000 and 94,600 cells per cc., the shells of all the other oysters were kept open during the entire experiment.

As the experiments progressed, we noticed that the oysters became sluggish and their responses to stimuli diminished. For example, if tapped with a glass rod, they would not close their shells as rapidly as under normal conditions. Sometimes the shell would not close at all, as if the tonus of the adductor muscle had been partially lost. This condition became more apparent as the experiment progressed perhaps indicating that the oysters exposed to strong concentrations of *Euglena* became partly paralyzed. Similar observations were made in the previous experiments where forms other than *Euglena viridis* were used. We thought that these conditions might be due partly to purely mechanical causes, such as clogging of the gills with a mass of cells which interfered with the respiration of the oysters, and partly to the toxic effects of the metabolites of the culture. We shall discuss this matter more fully in the latter part of this article.

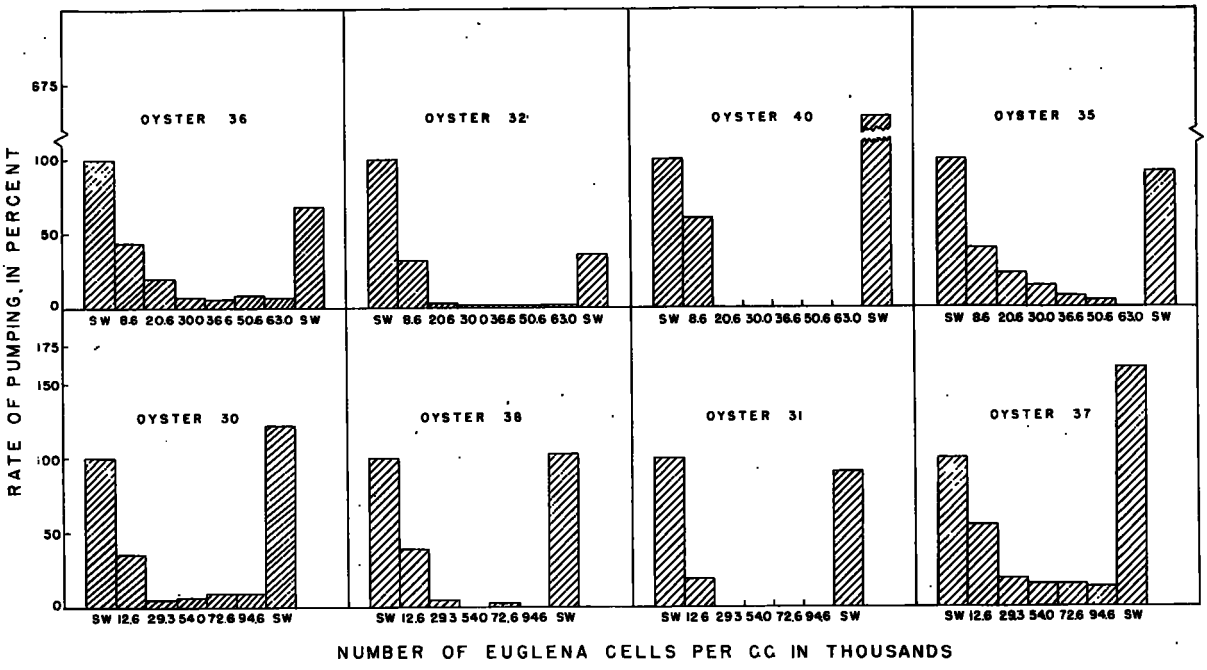

FIGURE 21.—Histogram showing rate of pumping (percentage) of oysters subjected to increasing concentrations of *Euglena*. The rate of pumping in sea water (SW) prior to exposure to *Euglena* was taken as 100 percent.

After the exposure to increasing concentrations of *Euglena* the oysters were again subjected to a flow of sea water. In all instances they soon resumed pumping, which at first was somewhat slow, but within a short period, rarely exceeding 30 minutes, became faster and reached a very rapid

rate usually during the second or third hour after the oysters had been returned to sea water. The post-exposure behavior of the oysters resembled the cleansing process observed in the earlier experiments where *Chlorella*, *Prorocentrum*, or *Nitzschia* were used.

RETAINING OF THE CELLS BY THE GILLS OF THE OYSTER

Our experiments offered us the opportunity to determine the number and percentage of cells retained by the oysters when these mollusks were feeding in different concentrations of *Chlorella*, *Nitzschia*, or *Euglena*. We accomplished this by comparing the numbers of the cells present in the water before and after it passed through the oyster gills. The method consisted in allowing the oyster to pump the water until we were certain that the overflow chamber (*G* in fig. 4) contained a true sample of the fluid passed through the gills, and then taking simultaneously two samples, one from the oyster chamber (*A* in fig. 4), where a continuous stream of a culture was running, and the second from the overflow chamber. Each sample was immediately checked with the Yoe colorimeter and the number of cells per cc. ascertained by reference to the curves used for the conversion of the microammeter readings into the number of microorganisms per cc.

In the experiments with *Chlorella* these determinations were made for a large number of oysters which were kept in concentrations ranging from 200,000 to 12,750,000 cells per cc. (fig. 22). The majority of the observations, however, were made with comparatively weak concentrations, because when strong ones were used the oysters either ceased pumping, or pumped at such a slow rate that it was often impossible to obtain reliable and large enough samples of water.

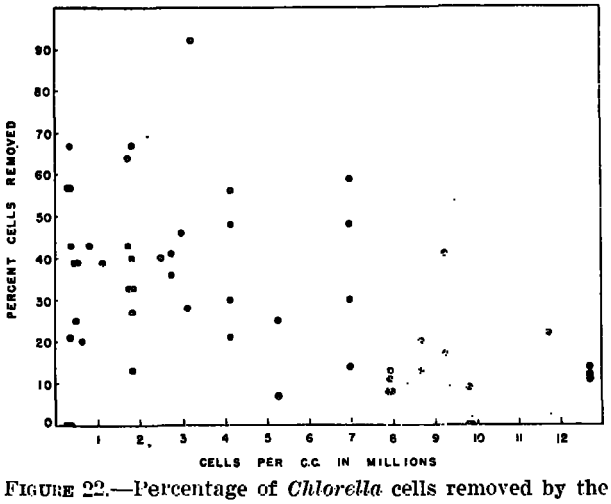

FIGURE 22.—Percentage of *Chlorella* cells removed by the oysters kept in different concentrations of this form.

Analysis of our data showed that the percentage of *Chlorella* cells retained by the gills of the oysters varied from 0 to 92. In the majority of oysters, however, less than 50 percent of the cells were retained. It appeared possible that in lighter concentrations the gills functioned more efficiently retaining a larger percentage of food organisms. However, this relationship was not very clearly defined (fig. 22).

Similar experiments were performed using *Nitzschia closterium* and *Euglena viridis*. In the experiments with *Nitzschia* we obtained data for concentrations ranging from 5 to 370 thousand cells per cc. The percentage of cells retained by the gills varied from 0 to 85. Usually more than 50 percent passed through the gills. In the experiments with *Euglena* the percentage of cells retained varied from 15 to 80. In neither case could we find a correlation between the number of cells originally present and those removed.

Incidentally, in our experiments we noticed that the pH of the water passed through the gills of the oysters was usually 0.1 or 0.2 lower than that of the water fed in the chamber containing an experimental oyster. The slight reduction of the pH was probably due to the removal of oxygen and to the addition of carbon dioxide to the water during its passage through the gills.

PRESENCE OF LIVING CELLS IN FECES OF OYSTERS

During this work we often noted that the feces of the oysters were composed almost exclusively of apparently living plankton organisms. Similar observations were made earlier on different lamellibranchs by other investigators.[7] To ascertain whether or not the plankton cells which passed through the digestive tract of the oysters underwent unfavorable physiological changes or suffered certain not easily detectable injuries we conducted the following experiments.

Oysters, the shells of which were cleaned of all attached material, were kept for 24 hours in sev-

[7] Blegvad 1914; Allen 1921; Churchill and Lewis 1924; Yonge 1926.

eral changes of sea water passed through bacteriological filters. When at the end of the period their digestive tracts were empty the oysters were placed to feed in sea water containing light concentrations of *Chlorella* or *Nitzschia*. Microscopic examination of the fecal ribbons which were soon formed by the oysters showed that they were composed of tightly packed cells of the species which was fed to them. Comparison of these cells with those constituting our standard cultures did not show any difference in color or structure. Many cells composing the feces were in the stage of active division, the condition indicating beyond all doubt that they were alive and uninjured.

Further proof of the healthy condition of the cells of *Chlorella* or *Nitzschia*, which passed through the digestive system of the oysters, was offered by the following experiment: small pieces of the fecal ribbons were carefully washed in five changes of filtered sea water and then placed in the culture media, where they were broken apart by vigorous agitation. Several days later the media flasks contained rich cultures of *Chlorella* or *Nitzschia*.

Thus, we were able to show that living plankton organisms can pass undamaged through the oyster gut. Yonge (1926) thought that this is possible because of the poor development of extracellular digestion in the oysters, and is especially due to the complete absence of extracellular protease and lipase. Petersen and Jensen (1911) and Blegvad (1914) maintained that the presence of living micro-organisms in the feces indicates that they are not important and perhaps useless as oyster food. This theory finds support in the work of Coe and Fox (1944), and Coe (1945) on the biology of the California mussel, *Mytilus californianus*. Coe (1945) thinks that the principal food supply of mussels "consists of minute particles of organic detritus derived from the disintegration of the cells of all kinds of marine organisms, both animals and plants, supplemented by living and dead unicellular organisms of minute size as well as living and dead gametes."

INHIBITING EFFECT OF THE CELLS AND OF THE LIQUID PORTION OF THE CULTURES

Our experiments gave sufficient evidence to prove that large quantities of micro-organisms present in the surrounding water adversely affect the oysters. Naturally, the question arose as to which component of a culture, i. e., the cells or the liquid, or perhaps the combination of the two, is causing the depressing effects. A review of the literature shows that numerous cases are known where an excessive growth of plankton was responsible for the unbalanced biological conditions which resulted in the mortality of aquatic animals. Prescott (1939) in discussing the relationship of phytoplankton to aquatic communities, stated that certain algae, while alive, liberate substances toxic to many forms. Decaying algae also produce large quantities of poisonous substances, such as hydroxylamine. Pratt (1942) in his extensive studies on *Chlorella vulgaris* found that these organisms manufacture and release in the surrounding medium a growth-inhibiting substance. This substance has not been identified as yet, but Pratt thinks that it is probably an organic base.

The mortality of oysters and other mollusks caused by the presence in the water of extremely large numbers of micro-organisms, usually dinoflagellates, has been observed in many parts of the world. Whitelegge (1891) reported a heavy mortality of oysters and mussels in Port Jackson, New South Wales, caused by *Glenodinium rubrum*. Nishikawa (1901) reports the destruction of pearl oysters in Japanese waters caused by *Gonyaulax polygramma*. Kofoid (1907) described the case of mortality of fish and shellfish occurring along the California coast, between San Pedro and San Diego, where *Gonyaulax polyhedra* was present in large numbers. Bückmann (1934) reported heavy injury to the oyster set of Helgoland caused by large numbers of the diatom *Skeletonema costatum*.

An interesting review of the literature on the occurrence of large numbers of dinoflagellates and their influence upon marine animals, especially mollusks, was recently offered by Nightingale (1936), who expressed the opinion that both the cells of micro-organisms and the products of their decomposition and metabolism may be fatal to marine animals. However, he did not arrive at a final conclusion regarding this matter, but suggested further studies of these problems.

To ascertain the relative importance of the cells and the fluid part of cultures in affecting the activities of oysters we carried on several experiments. We obtained *Chlorella* filtrate by filtering the culture through Berkefeld filters. To replace the

oxygen, which might have been lost during filtration, the fluid was afterwards vigorously aerated. Other methods employed to separate the cells from the medium, such as filtering through cotton, or through the finest grade of filter paper, or using the Foerst centrifuge, were unsatisfactory. The cells, owing to their small size, either penetrated through the filters or could not be separated by centrifuging.

Chlorella cells (residue) were collected also by using Berkefeld filters. After a large quantity of *Chlorella* had accumulated on the walls, we placed the filters in a vessel containing a very small quantity of water, and applied air pressure to drive the cells from the crevices of the filter. Usually the cells were used within one or two hours after having been filtered off. They were added to sea water in the quantities necessary to create the same concentration as that used at the beginning of the experiments, when unadulterated culture was used.

At first the oysters were placed in running sea water (fig. 23). Two hours after they opened and began to pump, a flow of a strong culture of *Chlorella*, containing approximately 10 million cells per cc., replaced the water. After another 2-hour period the flow of *Chlorella* was stopped and running sea water reintroduced. Thus, the effect of that particular culture of *Chorella* upon the oysters was determined. Upon elapsing of the second 2-hour period in sea water the oysters were subjected to a flow of filtrate of *Chlorella* which was obtained from the same culture, part of which was used earlier in the experiment. Then the oysters were again given running sea water for 2 hours, and finally subjected to *Chlorella* cells (residue).

The behavior of 16 oysters which we used in these experiments usually followed the pattern shown on the kymograph record reproduced in figure 23. It showed conclusively that the filtrate of the culture containing metabolic products of *Chlorella* cells, and the cells, affected the oysters. The rate of pumping was sharply reduced or even stopped when the oysters were subjected to either component.

A series of similar experiments in which we used a culture of *Nitzschia closterium* containing approximately 150,000 cells per cc. corroborated the results obtained with *Chlorella*. Each chief component of the culture, the cells or the filtrate, caused a reduction of the rate of pumping and changed the type of the shell movements of the oysters. Upon return from either one of these components to sea water the oysters soon showed a normal behavior.

EXPERIMENTS WITH YEAST

Our observations may be criticized on the assumption that the abnormal behavior of the oysters was perhaps caused by some of the ingredients of the media in which the microorganisms used in the experiments were grown. Such a criticism can be partly invalidated by pointing out that the material used for growing the culture contained no toxic substance. Furthermore, we applied the strict rule to use only those cultures which had been prepared long in advance, and where all signs of decomposition of fertilizing substances were absent. It was also our practice to aerate the cultures before using them, to be sure that no lack of oxygen existed and that the obnoxious gases which might have been present were driven off. Finally, we were able to show that even if the fluid part

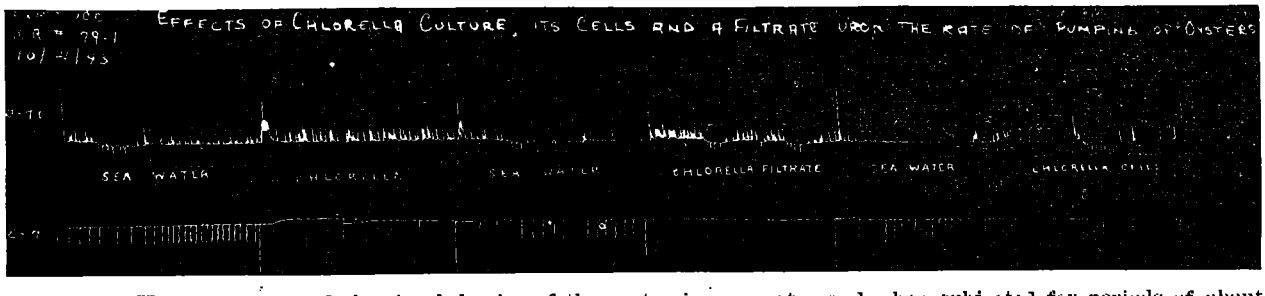

FIGURE 23.—Kymograph record showing behavior of the oyster in sea water and when subjected for periods of about 2 hours to a strong *Chlorella* culture of approximately 10 million cells per cc., to filtrate of *Chlorella*, and to cells of *Chlorella* suspended in sea water. Upper line shows the shell movement and the lower one, the rate of pumping of the oyster. Each short vertical line of the lower record represents 244 cc. of water pumped by the oyster.

of a culture were removed, the cells alone would, nevertheless, adversely affect the oysters. To substantiate further the latter conclusion we ran additional experiments in which cells of yeast instead of regular plankton micro-organisms were used. The yeast cells of the regular commercial variety were about 5 microns in diameter thus closely resembling in size those of *Chlorella*.

The experiments consisted in keeping the oysters for a period of about 3 hours in running sea water and then subjecting them for the same period to a flow of sea water to which a certain quantity of yeast had been added. The concentrations of yeast used were 0.1, 0.25, 0.5, 1.0, and 2.0 grams per liter. For each concentration records of seven or more oysters were taken. The temperature of the control sea water and of the sea water containing the yeast was near 20.0° C., the pH varied between 7.7 and 8.0, and the salinity was about 27.0 parts per thousand.

In the weakest concentration, containing 0.1 gram of yeast per liter of sea water, approximately one-half of the experimental oysters showed an increase in the rate of pumping which ranged from 51 to 240 percent over the original rate (table 3). The other half, however, showed a decrease ranging from 10 to 54 percent. The character of the shell movement was not noticeably changed by the introduction of yeast suspension.

In a concentration of 0.25 gram per liter, however, the depressing effect became quite evident (fig. 24). Of the 12 oysters used 11 showed a decrease in the rate of pumping ranging from 27 to 86 percent (table 3). In all heavier concentrations the presence of yeast cells in sea water always decreased the rate of pumping (table 3). In the concentration 0.5 gram of yeast per liter of sea water, the decrease ranged from 39 to 96 percent. In the concentration of 1.0 gram per liter the rate of pumping showed a decrease from 5 to 84 percent. In two-thirds of the oysters, however, the decrease was 63 percent or greater. In the strongest concentration, which contained 2.0 grams of yeast per liter of sea water, the reduction in the rate of pumping varied from 47 to 89 percent of the original rate. Therefore, the conclusion that the presence of a large number of micro-organisms in sea water compels the oysters to reduce the rate of pumping has been again confirmed.

In many instances after sea water was substituted for the yeast suspension the oysters displayed a very rapid rate of pumping (figs. 24 and 25). For example, two oysters pumped for a short period at the rate of 25,970 cc. per hour, while four others pumped from 20,916 to 22,550 cc. for the same period. It should be recalled that we noticed the rapid rate of pumping in our other experiments when the culture of micro-organisms, such as *Chlorella*, was substituted for sea water. Thus, we believe that sufficient data have been collected to show that this behavior, which may be considered as cleansing of the gills from the mass of cells and mucus, is of common occurrence among the oysters which were exposed to the water containing large quantities of suspended matter.

The exposing of oysters to a suspension of yeast of 0.25 gram per liter or heavier was invariably followed by a change in the type of the shell movements (figs. 24 and 25). Usually the contraction and relaxation of the adductor muscle becomes

TABLE 3.—*Effect of different concentrations of yeast cells upon the rate of pumping of oysters*

Oyster Number	Yeast concentration, gram per liter	Rate of pumping cc. per hour		Percentage of increase (+) or decrease (−) in rate of pumping in yeast suspension
		In sea water	In yeast	
6	0.1	1,027	1,602	+56
10	0.1	1,685	2,553	+51
91	0.1	7,735	6,949	−10
79	0.1	4,928	10,585	+115
93	0.1	4,335	6,600	+52
15	0.1	2,600	8,120	+212
54	0.1	2,456	8,342	+240
16	0.1	14,000	9,800	−30
2	0.1	12,611	3,713	+71
20	0.1	10,582	4,845	−54
19	0.1	10,950	8,906	−19
19	.25	12,358	6,630	−46
48	.25	2,066	1,033	−50
21	.25	8,493	1,773	−79
17	.25	10,349	6,478	−38
91	.25	14,933	3,080	−79
6	.25	1,343	1,343	0
79	.25	17,593	8,500	−51
10	.25	7,227	3,431	−53
54	.25	4,853	2,530	−48
51	.25	2,449	2,986	+22
93	.25	8,246	6,035	−27
15	.25	12,702	1,728	−86
95	0.5	10,956	396	−96
77	0.5	11,952	7,272	−39
92	0.5	9,204	4,758	−48
64	0.5	18,333	2,750	−85
96	0.5	13,197	7,844	−41
58	0.5	5,250	1,890	−64
91	0.5	11,466	3,042	−73
79	0.5	7,975	2,118	−73
47	1.0	2,158	2,063	−5
68	1.0	4,970	1,611	−68
94	1.0	10,179	3,276	−68
48	1.0	8,591	2,760	−68
80	1.0	5,291	1,412	−73
50	1.0	2,832	1,038	−63
52	1.0	4,950	797	−84
96	2.0	8,663	2,154	−75
93	2.0	5,565	2,451	−56
83	2.0	10,881	1,658	−85
80	2.0	2,213	699	−68
93	2.0	5,225	550	−89
83	2.0	21,200	2,562	−88
92	2.0	12,987	3,822	−71
80	2.0	2,148	1,141	−47

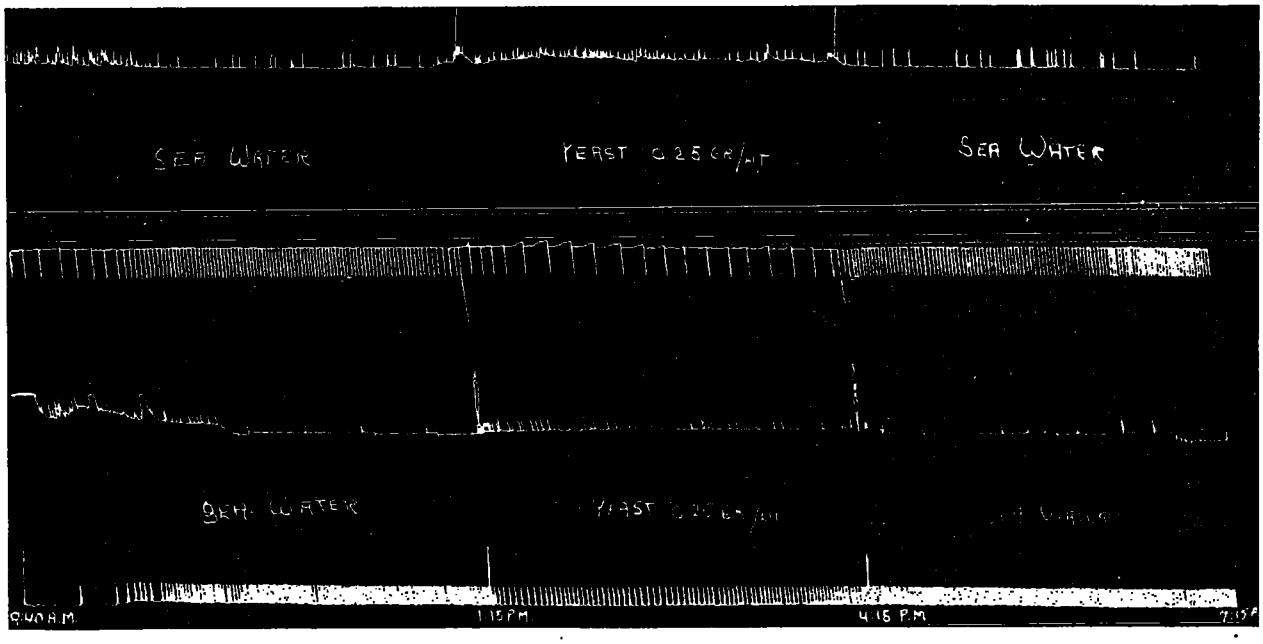

FIGURE 24.—Kymograph record showing effect of 0.25 gram of yeast per liter of sea water upon the shell movement (1st and 3d lines) and rate of pumping (2d and 4th lines) of two oysters. Each short vertical mark of the second line designates emptying of the tripping vessel of 280 cc., while each mark on the fourth line shows the dumping of 237 cc. of water.

more frequent. Nevertheless, in the majority of cases the shells remained open during the entire exposure while in the remaining instances the shells were closed only for very brief periods.

While in the suspensions of yeast the oysters formed very large quantities of pseudo feces which were composed almost entirely of yeast cells and mucus. The true feces, however, were formed in small quantities only. We noted that while the pseudo feces were white in color, the true feces were a dark brown. Microscopic examination of the feces showed that, in contrast to the pseudo feces, they consisted largely of plankton forms and detritus. These observations suggested that oysters exercise a certain degree of selectivity in their feeding. In some rare cases, however, the

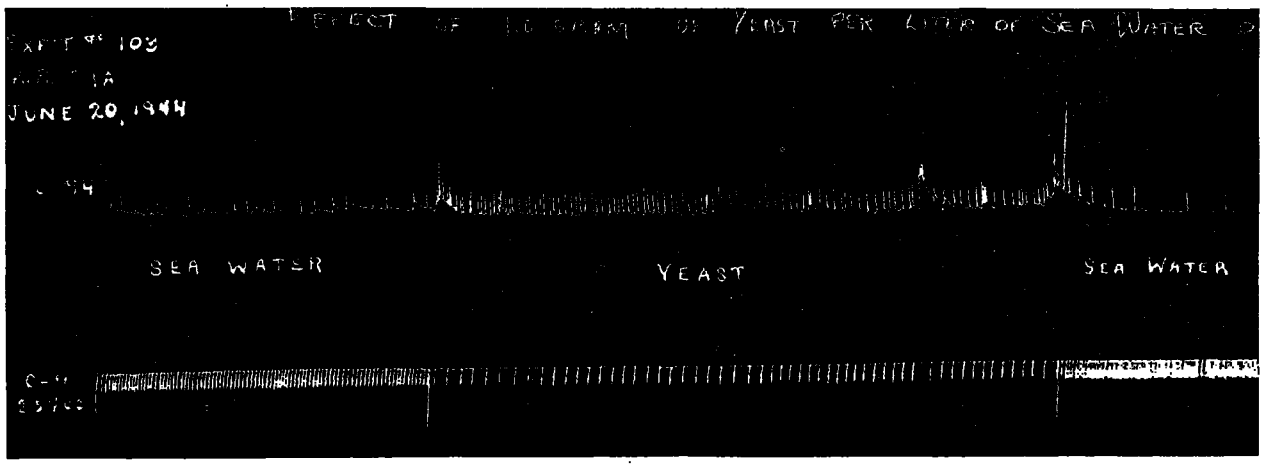

FIGURE 25.—Kymograph record showing effect of 1.0 gram of yeast per liter of sea water upon the shell movement (upper line) and rate of pumping of the oyster (lower line). Note the increase in the rate of pumping after the change from yeast suspension to sea water. Each short vertical line of the lower record represents 234 cc. of water pumped by the oyster.

feces were composed mostly of yeast cells. This indicated, perhaps, that the ability of food selectivity was not equally possessed by all oysters.

As in the experiments where *Chlorella*, *Nitzschia*, or *Euglena* were used, we made tests to find the relative quantities of yeast cells removed from suspension by the oyster gills. Although we did not count the number of yeast cells per cc. of water before and after it passed through the oyster, we formed, nevertheless, the quite reliable conclusion, by checking the samples with the Yoe colorimeter, that a relatively very small number of the yeast cells was retained by the gills, and that the largest portion passed through them and was expelled on the cloacal side of the oyster.

In general, this series of experiments showed that the behavior of the oysters subjected to a flow of sea water containing a large number of yeast cells strongly resembled that of the oysters exposed to heavy concentrations of plankton organisms, such as *Chlorella*, *Prorocentrum*, *Nitzschia*, or *Euglena*.

EFFICIENCY OF FEEDING AND FORMATION OF TRUE AND PSEUDO FECES

Our observations suggested that the relative quantities of true feces and pseudo feces formed by the oysters may indicate the efficiency of their feeding. To verify this the following experiments were run. Single oysters were placed in glass jars each containing 3 liters of *Chlorella* culture the density of which varied from 18,000,000 to 450,000 cells per cc. The different densities were made by diluting with sea water the original heavy culture, containing 18 million cells per cc. A control oyster was placed in a jar containing 3 liters of sea water. The oysters used were of almost uniform size, shape, and weight. Before being placed in the jars with *Chlorella* they were kept overnight in filtered sea water to have their digestive tracts emptied of the food.

During the experiment, which lasted three days, the temperature of the water in all the jars was the same ranging between 18.0 and 21.0° C., depending upon the room condition. The salinity in all jars was identical, being 26.55 parts per thousand. However, the pH of the different jars showed a difference. In the strongest concentration of *Chlorella* it was 8.3, whereas in the weakest one it ranged between 7.7 and 7.8, being identical with the pH of the sea water in which the control oyster was kept.

Our observations on the formation of true and pseudo feces by the oysters kept in different concentrations of *Chlorella* follow:

Concentration of 18,000,000 cells per cc.—The oyster opened its shells within a few minutes and soon began to expel large quantities of pseudo feces, although no true feces were discharged. After 35 minutes of activity the oyster shut its shells and remained closed until the end of the experiment. Apparently the concentration of the cells in the water was too great to allow the oyster to function normally. Therefore, after the initial effort of pumping the water, which resulted in the discharge of a large quantity of pseudo feces, the oyster stopped pumping and closed its shell. The density of the *Chlorella* population in the jar at the end of the experiment was practically the same as at the beginning. At the end of the third day we opened the oyster and found that its stomach was empty and the crystalline style was absent.

Concentration of 11,000,000 cells per cc.—The oyster opened and began pumping, forming pseudo feces 3 minutes after having been placed in the culture. When, after approximately 1 hour, the density of the culture had been somewhat reduced by the formation of pseudo feces, the oyster began to expel a small quantity of true feces. However, as in the previous concentration, the animal soon closed its shell, remaining inactive until the end of the experiment. The quantity of true feces formed during the active period was much smaller than that of pseudo feces. At the end of the experiment the stomach of the oyster was empty and there was no crystalline style.

Concentration of 5,400,000 cells per cc.—The oyster began pumping as soon as it was placed in the jar, ejecting a large quantity of pseudo feces. After a period of about 45 minutes the concentration of *Chlorella* was reduced to such an extent that the cells apparently ceased to interfere seriously with the feeding. As a result, a large quantity of true feces was gradually formed and finally the water was almost completely cleared of micro-organisms. We noticed that when the density of the culture was reduced to approximately 1,200,000 cells per cc., the formation of pseudo feces stopped almost entirely, while that of true feces proceeded uninterruptedly. The stomach of the oyster contained food and the crystalline style was present.

Exposure to this concentration showed that by forming pseudo feces the oyster was able to reduce the number of cells in suspension to approximately 1,500,000 cells per cc. and then proceeded to feed almost normally. We should emphasize, however, that the reduction of the number of cells was possible only because the oyster was kept in a small volume of water. Undoubtedly, if kept in a much larger vessel containing *Chlorella* of the same density as that existing at the beginning of the experiment, the oyster would be unable to reduce substantially the concentration of micro-organisms and would finally become inactive. It should also be remembered that in addition to the action of the cells, the fluid part of the culture would eventually contribute to the inhibition of the pumping activities of the oyster. We think, therefore, that the concentration of approximately 5,000,000 *Chlorella* cells per cc. should be considered as still being above the threshold which would permit the oyster to function normally.

Concentration of 3,600,000 cells per cc.—The observations made on the oyster exposed to this concentration were almost identical with those of the preceding one.

Concentration of 2,000,000 cells per cc.—The results obtained with this concentration closely resembled those of the two preceding ones with the exception that, because the number of cells was smaller the oyster could reduce it below the unfavorable level within a few minutes, and then proceed to eject true feces, the quantity of which greatly exceeded that of pseudo feces. Within a few hours the water in the jar was almost transparent.

Concentration of 1,200,000 cells per cc.—The oyster opened and began to filter water almost as soon as it was placed in the jar. The amount of pseudo feces formed was very small. The true feces, which were rather abundant, were dark green in color and were composed almost exclusively of *Chlorella*.

Concentration of 900,000 cells per cc.—The results of this experiment were almost the same as those observed in the previous concentration with the exception that even less pseudo feces were formed.

Concentration of 450,000 cells per cc.—The plankton content of the water was quickly ingested by the oyster and discharged in the form of true feces. No pseudo feces were produced. This probably indicated that the animal was able to feed very efficiently.

Control—sea water.—The oyster placed in sea water utilized almost the entire content of micro-organisms within a very short time. The brown feces consisted mostly of the organisms commonly found in sea water. No pseudo feces were formed.

Experiments of the same nature were performed on two more occasions. New oysters were used but the concentrations chosen closely approximated those of the first experiment. The results of all three experiments were in agreement with the exception that in the strong concentrations of the last two experiments some of the oysters remained open but apparently not pumping because neither feces nor pseudo feces were formed.

These experiments showed once more that heavy concentrations of *Chlorella*, containing more than 5 million cells per cc., seriously interfere with the oysters which cease pumping if kept in such a concentration for long periods. In intermediate concentrations, ranging from approximately 2 to 5 million cells per cc., the oysters may continue to feed. However, the rate of feeding is low because the activity of oysters is directed primarily to the cleansing of their gills, and results in the formation of a very large quantity of pseudo feces. If these conditions persist, the oysters may eventually become inactive.

In light concentrations, containing less than 2 million *Chlorella* cells per cc., the oysters feed normally. Under these conditions the quantity of true feces ejected is relatively large, while pseudo feces are either absent or formed in very small quantities.

On the basis of these and the previously described experiments we may formulate a general rule, namely, that the quantities of pseudo feces formed by the oysters are usually roughly proportional to the quantities of plankton and other material suspended in the water, whereas a reverse relationship exists in the formation of true feces. The latter relationship, naturally, does not include the condition when the water is devoid, or almost devoid, of suspended matter.

The presence of large quantities of pseudo feces also indicates that the feeding of oysters proceeds under unfavorable conditions caused by heavy concentrations of material suspended in the water. Small quantities of pseudo feces, or their absence, in the presence of large quantities of true feces

show, on the other hand, that the oysters are feeding efficiently.

The concentrations of cells which began to interfere noticeably with the normal feeding activities of the oysters varied with the different species, depending upon the size of the micro-organisms. In general, the larger the size of the micro-organisms, the smaller the number necessary to create unfavorable conditions. Obviously, because of the great variety of plankton forms in sea water, it is impossible to determine the maximum concentration of each species that could be tolerated by the oysters. The problem becomes even more difficult when it is remembered that in nature it is not a single species but a combination of many which usually populates the water where oysters exist. We think, however, that during these studies we found a general criterion which we believe may permit us to determine the lowest concentration of a single or of a combination of different plankton forms which would depress the normal rate of pumping of the oysters. This criterion is based upon the determination by the Yoe colorimeter (Yoe and Crumpler 1935) of the relative density of the plankton population in the water. Within the scope of our experiments we found that regardless of the type of species, or of their size, the oysters began to show signs of abnormal behavior when, because of the presence of micro-organisms, the turbidity of the water, as registered on the microammeter, dropped below the 23 mark. This point corresponded to approximately 2,000,000 *Chlorella*, 70,000 *Nitzschia*, or 3,000 *Euglena* per cc. of water. Of course, as should be expected, the individual variations among the oysters were of considerable magnitude.

DISCUSSION

It is axiomatic that the physiological behavior of an animal depends upon and is controlled by changes of its environment. In the case of the oyster, *O. virginica*, which lives either in the intertidal zone or in comparatively shallow water affected by the tides, the changes are frequent and often abrupt. Because of the tidal currents flowing over the beds the quantity and quality of the micro-organisms change almost continuously. The seasonal changes in the plankton population diversify even greater the variety and concentrations of the microscopic forms. Thus, as far as the quantity of food supply is concerned, the oysters are subjected to an almost continuous change and, therefore, must be equipped anatomically and physiologically to cope, within certain limits, with the change of the condition.

As mentioned earlier, Yonge (1936) expressed the opinon that oysters evolved from forms which lived in clear water, but gradually developed a more efficient cleansing mechanism that enabled some of the species, such as *O. virginica* and *O. angulata*, to exist in less clear waters. However, in the opinion of some investigators (Kellogg 1915) this tolerance of the oysters is still very limited, the animals being able to feed only when the water contains in suspension relatively small quantities of food organisms or other materials. Grave (1916) and Nelson (1921, 1923) on the contrary, maintained that oysters would feed rapidly in water bearing large quantities of suspended matter. The results of our experiments indicate that both schools of thought are correct but only to a certain extent.

The opinion advanced by Kellogg is fully supported by our experiments in the respect that oysters will feed efficiently only if the water contains small quantities of suspended material. Contrary to Kellogg's opinion, however, we found that oysters are also capable of feeding, at least for short periods, in heavily laden water. Under such conditions, nevertheless, the rate of feeding is depressed. Consequently, the conclusions of Grave and Nelson (loc. cit.) could be considered correct only if they were qualified with additional statements emphasizing the time element and showing that the efficiency of feeding of oysters decreases in water too rich in micro-organisms. Since no such statements were made by those authors, their conclusions create the impression that it is unimportant whether or not the water is clear or heavily laden.

Nelson's opinion (1923) that the rate of water filtration by oysters is independent of the quantity of material suspended in the water cannot be corroborated by our studies, which gave ample evidence that, in general, the rate of pumping decreases with an increase in the number of micro-organisms. We think that Nelson's conclusions were formed because of the wrong interpretation of his experimental data. Nelson's (1921) experiment, as recently pointed out,[8] was designed to

[8] Loosanoff and Nomejko 1946.

study only the shell movements of oysters and not the rate at which these mollusks were pumping water. Obviously, because he had no data on the rate of pumping, which is the criterion of feeding, no definite conclusions should have been formed regarding the latter subject. Nevertheless, assuming that the frequent and rapid closing and opening of the shells signified active pumping and feeding, whereas they actually might have shown repeated ejection of pseudo feces, the phenomenon indicating that the efficiency of feeding was reduced, Nelson (1921, 1923) concluded that the rate of filtration of water is independent of the quantities of material suspended in the water.

As shown in the earlier part of this article, there are rather definite concentrations of the micro-organisms above which the feeding of oysters was inhibited. In concentrations below this threshold, the rate of pumping was not reduced, and often the rate of pumping of the oysters kept in light concentrations was even greater than when they were kept in running sea water. In concentrations above the threshold, however, a reverse correlation was noticed between the density of micro-organisms and the rate of pumping. In heavy concentrations pumping entirely ceased. Under such unfavorable conditions little or no food was ingested by the oysters and the crystalline style was usually absent. The oysters were forming large quantities of pseudo feces to cleanse their gills and palps of the excessive accumulation of food cells.

Upon coming in contact with the large number of micro-organisms the type of shell movement of the oysters changed, showing frequent attempts to expel the masses of cells and mucus accumulating on the gills and palps. Under these conditions the shells often remained open for long periods although no water was pumped.

In many of our experiments we noticed cessation of pumping when the oyster shells were open and the edges of the mantle were widely separated. Therefore, the decrease in the rate of pumping, or its complete cessation, could not be attributed to the fact that the water could not enter the gill cavity of the oysters because the latter was blocked by the edges of the mantle.

The results of our experiments at first appeared to be rather paradoxical. They showed that the rate of feeding of oysters decreased when plankton was heavy, while if given only a limited quantity of food, the oysters acted normally. Our conclusion contradicted the established opinion that a rich plankton population was necessary for a favorable existence of these mollusks. For example, Nelson (1921) stated "Any conditions which result in an increase in the number of food organisms in the water will make for fatter and better oysters." Naturally, an explanation was needed to clarify our conclusions. We offer this explanation by referring to our experiments which showed that large numbers of micro-organisms in sea water affect the oysters mechanically, by interfering with the proper functions of the gills and palps, and also chemically. The latter apparently is due to the presence of a certain inhibiting substance released by micro-organisms in the surrounding water. At present we do not know the nature of this substance, but we have determined that it is heat resistant, and that vigorous aeration for a period of 24 hours does not reduce its toxicity.

The mechanical interference apparently causes a disturbance of the synchronization of the ciliary motion and results in a decrease in the flow of water through the gills. Detailed studies of these phenomena, as well as of the chemical effects of the filtrates of the various cultures of micro-organisms upon the mantle gills, palps, and adductor muscles of the oysters, will be discussed by Loosanoff in a separate article. It is sufficient to say here that the gills of the oysters kept in water rich in plankton became quickly covered with a mass of food cells which imbedded in the gill mucus. This interferes with the normal feeding of the oysters and, probably, with their respiration. In extreme cases the mass of micro-organisms covering the gills, undoubtedly, was slowly suffocating the oysters. Miyake, whose report was not available to us but whom Nightingale (1936) mentions in his paper, came to the same conclusions while studying the mortality of the pearl oyster in 1933 in Gakasho Bays, in Toba, Japan. He found that losses among pearl oysters, estimated at 15 million yen, were caused by clogging of the respiratory organs of the mollusks with a mass of *Gymnodinium*.

In our experiments the oysters exposed to dense cultures of micro-organisms were trying to keep their gills and palps clean. This was shown by the characteristic movements of the shells directed to expel large quantities of pseudo feces. At the same time little or no true feces were formed, which indicated that little or no food was ingested.

These and the observations mentioned in the preceding paragraph provide the explanation as to why the presence of a rich population of micro-organisms creates an unfavorable condition for the existence of oysters.

Our conclusions agree with those of Kellogg (1915) who found that when relatively large quantities of suspended material were collected by the gills of the oyster and then brought to the palps all or most of this matter was rejected and expelled as pseudo feces. Yonge (1926) also observed that if the gills of an oyster were heavily covered with a mass of particles, these particles, regardless of their individual size, would be all removed before being carried to the mouth.

Our laboratory experiments were to a large extent corroborated by observations on the conditions existing in nature. For example, it has been observed that the oysters of Great South Bay in the State of New York have been poor for several years. During the same period, however, the water of the bay was extremely rich in plankton. Nevertheless, regardless of the presence of large quantities of food the oysters remained poor. Joseph B. Glancy, who studied the conditions in Great South Bay, told us that the oysters usually become poor when micro-organisms are present in large numbers. Perhaps other undiscovered factors also contributed to the poor condition of the oysters of that body of water, but the fact remains that they were in such a state regardless of the abundant food supply.

As an example of the opposite type, we may mention Gardiners Bay, Robin Island Sound, Shelter Island Sound, and other basins of the State of New York where the water is usually very clear containing but a small number of micro-organisms. Yet it is a well known fact to the members of the industry and to the biologists working in this vicinity that these basins are used to improve the condition of the oysters which in those waters accumulate large quantities of glycogen. Thus, despite comparatively small numbers of micro-organisms, the oysters of those areas become "fatter" than those living in water much richer in plankton, such as Great South Bay.

Perhaps the most interesting and significant conclusion may be made from a letter received by the senior author in April 1946 from P. O. Mercer, manager of the largest oyster company of Great South Bay, which states: "It is true that the meats of the oysters in Great South Bay have been of excellent quality during the past year. The water in the bay has been and is still unusually clear which indicates that the microscopic organisms which were in the water during the last several years have disappeared."

In connection with the discussion we would like to mention that recent plankton studies of Long Island Sound, carried on by Riley (1941), showed that plankton was least abundant during October, November, and the early part of December or, in other words, during the period when the oysters in our waters accumulate large quantities of glycogen. This observation appears to be of considerable significance perhaps indicating nature's provision to create more favorable conditions for the oysters during the season when large quantities of glycogen should be stored in their bodies.

In nature the appearance of masses of micro-organisms dense enough to kill the oysters in a short time is of rather rare occurrence but was, nevertheless, noticed in a number of cases in different parts of the world (loc. cit.). The presence of relatively heavy concentrations, not dense enought to kill the oysters within a short time, but heavy enough to interfere with their normal existence and to make them poor has also been observed. For example, during the seasons when the water of Great South Bay contained over 3,000,000 cells of small green algae per cc. the oysters were usually very poor. We realize, however, that such cases are of unusual nature, and that the numbers of micro-organisms in the water flowing over the oyster beds are considerably smaller than those found in Great South Bay or employed in some of our experiments. Nevertheless, our studies showed that the feeding of oysters proceeds efficiently only when the water is relatively clear. The appearance of micro-organisms in numbers exceeding the threshold suggested in this article unfavorably affects oysters by depressing their rate of pumping and, therefore, feeding.

Before advancing final conclusions, however, more research on the subjects discussed in our paper is necessary. Thus far, our studies have been confined to oysters of the same general locality, living under approximately the same conditions. Consequently, it is not known whether the conclusions which we offer would apply to oysters of other geographical areas, where environmental conditions are radically different

from those of the New York and New England beds. We also are well aware of the existence of "claires" at Marennes and other places along the French coast where oysters, although of different species than ours, are fattened in the presence of abundant supplies of diatoms, peridinians, algal spores, and other micro-organisms. Obviously, further extensive studies are needed before final conclusions may be safely and correctly formed.

SUMMARY

1. Experiments performed with *Chlorella* sp., *Nitzchia closterium*, *Prorocentrum triangulatum*, *Euglena viridis*, and a common variety of yeast have demonstrated that there are rather definite concentrations of these forms above which the density of the micro-organisms begins to interfere with the feeding of the oysters.

2. In heavy concentrations of micro-organisms the rate of water pumping of the oysters was reduced, and the character of the shell movement noticeably changed. In many instances a correlation was noticed between the density of the micro-organisms and the rate of pumping. Pumping entirely ceased in very heavy concentrations.

3. When the cells were too abundant little or no food was ingested by the oysters and the crystalline style was usually absent. The oysters were forming large quantities of pseudo feces to cleanse their gills and palps of an excessive accumulation of plankton cells.

4. In concentrations below the threshold the rate of pumping was not reduced and the shell movements remained normal. In many instances the rate of pumping of the oysters kept in light concentrations of micro-organisms was even greater than when kept in sea water.

5. The size of the cell played an important part in affecting the activities of the oysters. A much greater number of small-sized cells, such as *Chlorella*, was needed to produce the same effect as caused by a smaller number of larger organisms, such as *Euglena*.

6. In heavy concentrations of micro-organisms the shells of the oysters sometimes remained open for periods of several hours although no water was pumped.

7. If the oysters were kept in heavy concentrations for prolonged periods, the tonus of the adductor muscle became impaired or partially lost. The oysters became sluggish and their responses to stimuli diminished.

8. Both the filtrate of the cultures, containing metabolic products of the cells, and the cells were found to affect the oysters. The rate of pumping was reduced or entirely stopped when the animals were subjected to strong concentrations of either component.

9. When, after exposure to heavy concentrations of micro-organisms the oysters were again subjected to a flow of sea water, their rate of pumping usually showed a marked increase. Such intensive pumping on the part of the animals suggested an attempt to cleanse themselves of the micro-organisms which had accumulated in the gills and mantle chamber.

10. The percentage of cells of *Chlorella* sp. removed by the gills of the oysters during the feeding processes varied from 0 to 92. In the majority of cases, however, less than 50 percent of the cells were retained. In the case of other micro-organisms usually more than 50 percent of the cells passed through the gills. No correlation was found between the number of cells originally present in the water and those retained by the gills.

11. The oysters exercised a certain degree of selectivity in their feeding. This ability, however, was not equally demonstrated by all the oysters.

12. It has been observed that living plankton organisms, such as *Chlorella* and *Nitzschia*, can pass undamaged through the digestive system of the oyster.

13. The quantities of pseudo feces produced by the oysters were usually roughly proportional to the quantities of plankton and other materials suspended in the water, whereas a reverse relationship existed in the formation of true feces.

14. The presence of large quantities of pseudo feces usually indicated that feeding of oysters proceeded under unfavorable conditions caused by heavy concentrations of material suspended in the water. Small quantities of pseudo feces, or its absence, in the presence of large quantities of true feces showed that the oysters were feeding efficiently.

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UNITED STATES DEPARTMENT OF THE INTERIOR, J. A. Krug, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

ECOLOGICAL AND PHYSIOLOGICAL STUDIES OF THE EFFECT OF SULFATE PULP MILL WASTES ON OYSTERS IN THE YORK RIVER, VIRGINIA

By PAUL S. GALTSOFF, WALTER A. CHIPMAN, Jr., JAMES B. ENGLE
and HOWARD N. CALDERWOOD

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Ecological and Physiological Studies of the Effect of Sulphate Pulp Mill Wastes on Oysters in the York River,[1] Virginia

For more than a quarter of a century the oyster industry of the York River in Virginia has experienced a gradual decline resulting from poor quality of the oysters, particularly from the upper section. This decline in the yield of oyster bottoms has brought severe losses and hardship to many people dependent on this industry for a means of livelihood. Numerous requests were made from time to time for the former United States Bureau of Fisheries, now a part of the Fish and Wildlife Service of the Department of the Interior, to determine the cause of the poor quality of the oysters. The first request was made in December 1916, when many of the oyster planters of the York River drew up a resolution expressing their belief that the discharge of wastes by a paper mill established at West Point, Va., in 1913, was damaging their oysters. They urged that the Federal Government investigate the cause of the failure of their oysters to grow and fatten. In response to this request, the first survey of the York River oyster bottoms was made in September 1917 by L. H. Almy, fish pathologist of the Bureau of Fisheries. After determining the salinity, alkalinity, and the dissolved oxygen content of the water at three stations near West Point, he arrived at the conclusion that the pulp mill was not at that time polluting the river "with any material which can in any manner affect the growth of oysters." He admitted, however, that some subtle change had taken place in the York River, the extent and nature of which could not be determined.

In 1918, another investigation was made by E. P. Churchill and J. S. Gutsell of the Bureau of Fisheries, in cooperation with W. W. Skinner and J. W. Sale of the Bureau of Chemistry, Department of Agriculture. In the course of these studies three trips were made, in winter, spring, and late summer, to collect samples of water, mud, and oysters at different stations. So far as the solution of the problem is concerned, the investigation produced negative results for it failed to arrive at any definite conclusion. No heavy metals which may be toxic to oysters were found in the samples of water, and the presence of sulfites and sulfides, which may exert deleterious effects on oysters, was not demonstrated in the effluents, presumably because no field tests for these oxidizable substances were carried out and the samples were examined only in the laboratory. The investigators suspected, however, that extractive matter of the pulp-mill effluent may have contributed indirectly to the destruction of oysters. They also stated that "the appearance of the condition of oysters * * * suggests the possibility of a depleted food supply and that the oysters are actually starving" but "are not being directly injured by the effluents from the mill."

It was obvious from the results of the two surveys that the York River conditions presented a very difficult and complex problem which could not be solved by casual ecological observations or by analyses of the samples of oyster-meats, mud, and water collected incidentally from a few stations. The solution of the problem called for well-planned and long-continued field and laboratory studies on the biology and physiology of the York River oyster, and chemical investigations into the nature of the pulp-mill wastes. An investigation of this type involves systematic ecological observations, physiological experimentation, and chemical studies. A well-equipped shore laboratory, special field equipment, and suitable boats are needed for the conduct of such a research problem.

Funds for the York River investigations were made

[1] Approved for publication October 11, 1946. Fishery Bulletin 43.

available in 1935 by a special allotment from the Public Works Administration. Continuation of the project was made possible by regular allotments by the Bureau of Fisheries and appropriations from the Commonwealth of Virginia through its Commission of Fisheries. In October 1935 a laboratory was established at Yorktown, Va., where a satisfactory supply of sea water was available for physiological studies on oysters. A boat suitable for the field observations was supplied by the Virginia Commission of Fisheries. Studies of the chemical nature of the pulp-mill effluents were carried on from July 1938 to July 1940 at laboratories made available by the College of William and Mary.

The general plan of the investigation was outlined by Dr. Paul S. Galtsoff, who is responsible also for developing the technique of bioassays employed in testing the effects of pollutants on the rate of pumping of water by oysters. The largest part of the laboratory and field work was carried out by Dr. Walter A. Chipman, Jr., in cooperation with Dr. Arthur D. Hasler, who participated in this project from October 1935 to June 1937. James B. Engle was engaged from June 1936 to July 1937 in field observations on methods of oyster cultivation employed by local oyster growers, and participated in other routine laboratory and field work. Dr. Howard N. Calderwood, who joined the staff in July 1938, conducted chemical studies of the pulp-mill effluents and was responsible for the fractionation of the pollutant and preparation of extracts used in the bioassays. Pathological studies of the York River oysters and analyses of experimental data on the effect of the pollutant on the physiology of the oyster were made by Dr. Paul S. Galtsoff with the assistance of Mrs. Dorothy H. Algire, formerly a junior zoologist of the Service. The authors are indebted to Dr. Chester I. Bliss for his advice regarding the evaluation of experimental data, and to Dr. L. B. Tuckerman of the National Bureau of Standards, for the computation of the possible accumulation of the pollutant in the York River tidal basin.

The work of establishing the laboratory and installing a sea-water system and other equipment was accomplished by Dr. Nelson A. Wells during the first few months of the investigation. In the course of the laboratory and field work, assistance was given also by Lloyd R. Garriss, Robert O. Smith, L. Winder Lane, and Alfred R. Armstrong. Valuable cooperation was rendered by the late Richard Armstrong, commissioner of the Virginia Commission of Fisheries, and his successor, the late G. Walter Mapp, and the staff of the commission. To H. A. Marmer and other members of the United States Coast and Geodetic Survey the authors are indebted for the use of some of the instruments needed for hydrographic observations, and analyses of the data of tidal-current observations in the York River. The oystermen of the vicinity have been extremely helpful in giving information regarding methods of oyster culture and in permitting the examination of their books and records. Officials of the Chesapeake Corp. have been very kind in supplying information and providing samples of pulp-mill wastes to the investigators. The authors also wish to thank J. J. Dirzulaitis, of the United States Geological Survey, for the loan of equipment, and Stewart Richardson and W. L. Howlett for their assistance in obtaining water and oyster samples.

PLAN OF INVESTIGATION

An investigation into the causes of the decline in the productivity of shellfish grounds should take into consideration various possibilities. Abnormal changes in the appearance, growth, and chemical composition of shellfish may be due to a functional disease, the presence of pathogenes, or infestation by parasites or commensals; they may be a result of adverse conditions caused by sewage pollution, the presence of poisons in the water, or some other environmental factor. On the other hand, an indirect effect brought about by man's activities should not be overlooked. Changes in ecological conditions of the river, and consequently in the productivity of its bottom, may be caused by deforestation of its drainage area, increased sedimentation, dredging of channels, and other improvements for navigation. To provide a basis for conculsions, observations made in waters suspected to be affected by pollution should be compared with those made simultaneously in another body of water which is known to be free of pollution. These control observations may be of great use in eliminating from consideration the factors present in both streams and in determining those which are primarily responsible for the decline of the fishery. Furthermore, the decline may be the result of depletion of natural resources due to lack of management and unsatisfactory methods of cultivation. All these possibilities have been taken into consideration by the investigators.

In the present investigation attempts were made to follow the natural course of events in the York River by observing seasonal changes in temperature, salinity, pH, oxygen content, currents, phosphates, and plankton. Parallel observations were carried out in the Piankatank River, which was selected for its proximity and similarity to the York River from the ecological point of view. By conducting these observations it was expected that a comparative study of the principal ecological factors operating in the two rivers might reveal the existence of some distinct differences, such as deficiency of food, lack of oxygen, etc., which would explain the poor condition of the York River oysters.

The biology of the oyster in the York River was studied in detail with special attention to the time and intensity of spawning and setting and to glycogen accumulation in oysters grown in various sections of the river. A number of field tests were conducted to determine the changes in glycogen content of York River oysters removed from the polluted area and in the seed oysters from James River planted in polluted and nonpolluted sections of the York River and in the Piankatank.

Since the official statistics of the oyster fishery cover large administrative areas and therefore are not available for the York River separately, special efforts were made to obtain authentic data from individual oyster planters and dealers who consented to submit their records and books for examination. By analyzing and separating these data it was possible to report on the condition of the oyster industry in the York River during the last 30 years.

Thorough examination of abnormal oysters was made for evidence of disease, parasitic infestation, or other pathological conditions that might be found from detailed microscopic study of the various organs and tissues. Because of the abnormal condition of the shells, detailed examination was made of the structure of the shell material.

Laboratory investigations consisted in determining the direct physiological effect of pulp-mill wastes on oysters and on the growth of a diatom *Nitzschia*, which is used by oysters as food and is frequently found on oyster grounds. Using the technique developed in previous work, records were obtained of the shell movement, efficiency of ciliated epithelium, and rate of filtration of water through the gills in clean water and in water containing known amounts of pulp-mill wastes.

Observations made during the first year of these studies showed that the pulp-mill effluent has a distinct physiological effect on oysters. In the following years attempts were made by Dr. Calderwood to explore the chemical nature of these complex materials with the view of isolating, if possible, the specific compound or compounds producing this physiological response, determining their chemical and physical properties, and rendering them harmless. This chemical investigation was closely coordinated with the experimental studies of the effect of various fractions of the pulp-mill effluent on the physiology of the oyster.

DESCRIPTION OF THE YORK RIVER

GEOGRAPHICAL AND GEOLOGICAL

The York River system, composed of the York River and its two chief tributaries, the Pamunkey and Mattaponi, together with their tributaries, is situated in central Virginia between the watersheds of the Piankatank and Rappahannock Rivers on the north, and the James Basin on the south. The drainage area of the York River system is shown on the map in figure 1. According to the United States Engineers (1930), the total drainage area is 2,663 square miles, of which about 90 percent, 2,386 square miles, are drained by the two rivers, the Pamunkey and the Mattaponi, whose confluence forms the York River at West Point. The two chief tributaries of the Pamunkey River are the North and South Anna Rivers, which have their origin in the foothills of the Blue Ridge and flow in a southeasterly direction through the Piedmont Plateau to the fall line and into the coastal plain, joining to form the Pamunkey a short distance from Ashland. The Mattaponi River is composed of the union of a number of small branches originating in Spotsylvania County. This river drains the eastern portion of the area and joins the Pamunkey at West Point.

Within the flat coastal plain the rivers are in broad valleys, the lower reaches of which meander through many miles of low country flanked by marsh lands from ¼ to 2 miles wide on either side. Almost one-half of the watershed lies within the Piedmont Plateau and is characterized by an irregular rolling topography with the streams confined to narrow valleys.

The York River (fig. 2) is a brackish estuary, an arm of the Chesapeake Bay, noteworthy for its very deep channel and the directness of its course. At

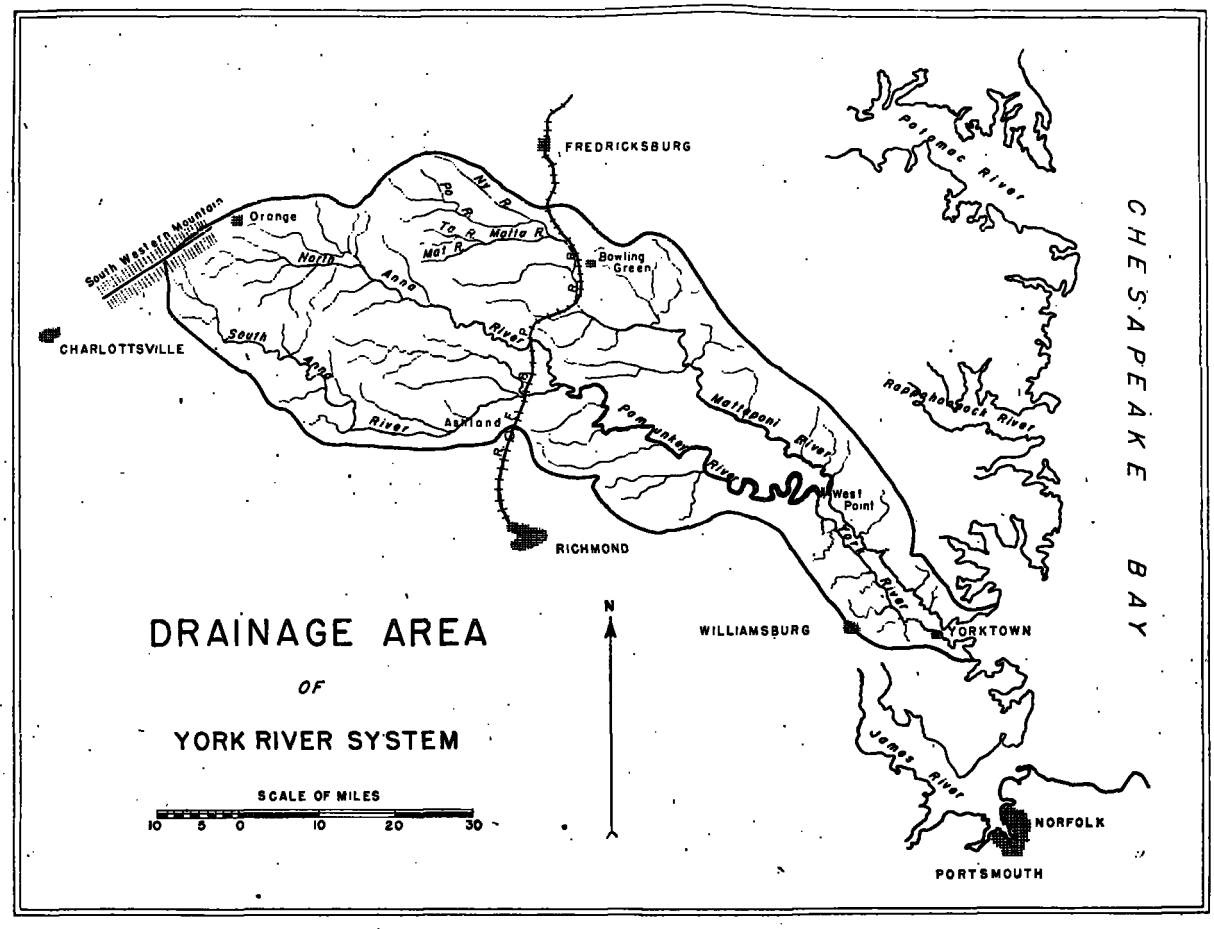

FIGURE 1.—Drainage area of the York River system. Reproduced from Document 54, Seventy-first Congress, United States House of Representatives, Pamunkey River, Va., York River system, figure 1: 1.

West Point the width of the river is 1¼ miles, and in its southeastward course of 26 miles to Yorktown the average width is 1.7 miles. Below Yorktown, the course is easterly for 7 miles and then southeasterly for another 7 miles, the river emptying into the Chesapeake Bay about 20 miles from the Atlantic Ocean and 15 miles north of Hampton Roads. As for depth, it has a navigable depth of 30 feet to within 9 miles of West Point and 35 feet to Yorktown. Improvements by the Federal Government, started in 1881, allow a navigable depth of 22 feet at low water at West Point, and depths of 6½ feet for 33 miles in the Mattaponi, and of 7 feet for 50 miles in the Pamunkey.

The creeks draining into the York River are small and inconsequential. Their presence, however, aids in the formation of the food supply for the oysters which are planted in beds in the shallow water bordering the river banks. The banks of the river are nearly parallel, and the few bays and inlets are of little importance. Purtan Bay, on the left shore, comprises about 275 acres and has a semistiff bottom used for the cultivation of oysters. Three small creeks enter Purtan Bay. Poropotank Bay, on the same side of the river about 3 miles above, is formed by the widening of the Poropotank River and is somewhat smaller. This bay is also used for the growing of oysters.

The oyster grounds of the York River are found on the flats on both sides of the river from the mouth to the head and, in a few instances, in deeper water where the bottom is of suitable nature. The largest part of the oyster-producing bottom is leased from the State by private interests. There are, however, about 800 acres of natural "rocks" owned by the State and open to the public for tonging. The names and locations of these "rocks" are: Green Point Rock, from Gloucester Point to Green Point; Pages Rock,

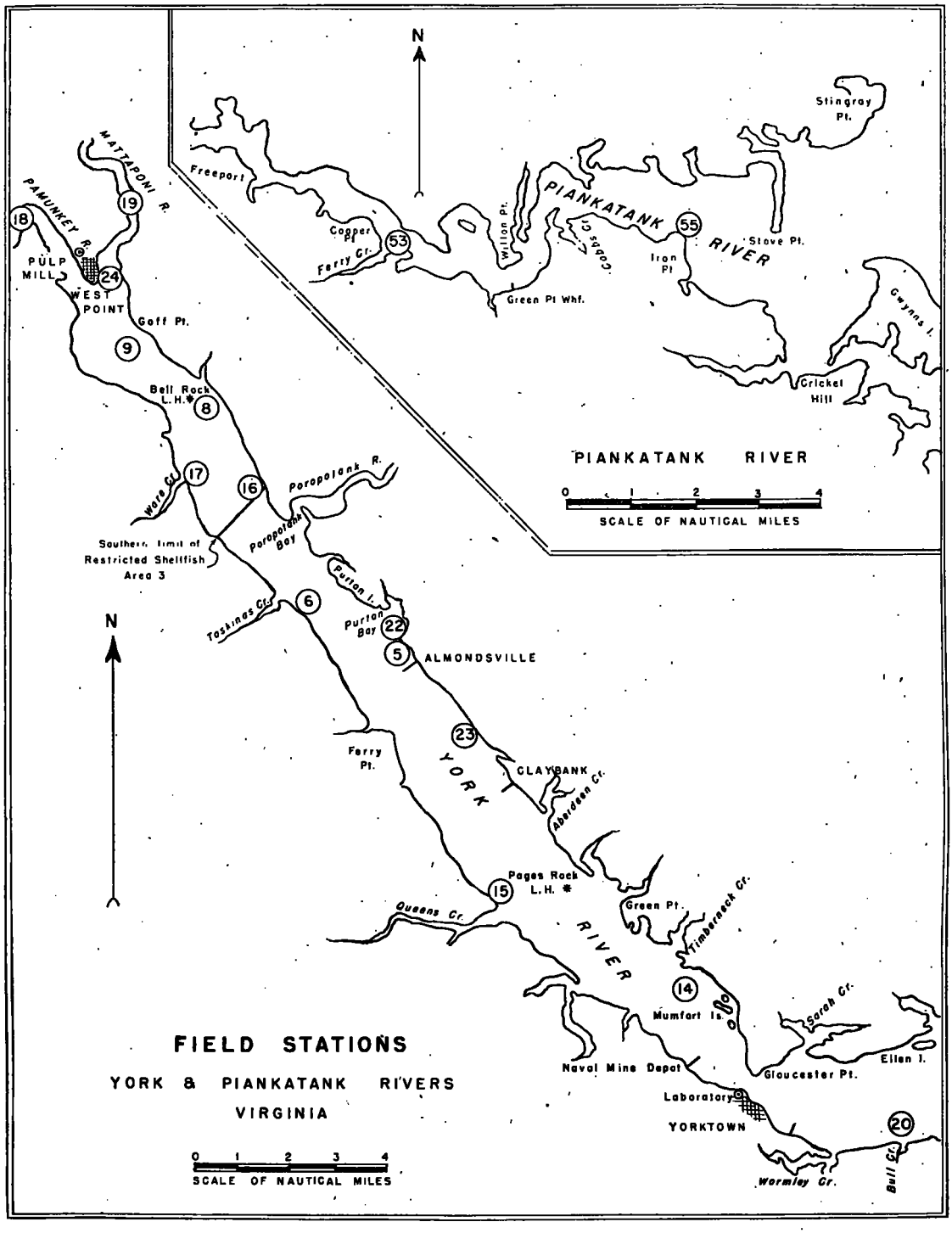

FIGURE 2.—The York and Piankatank Rivers. Sampling stations are indicated by numbers in circles.

from Green Point to Aberdeen Creek; Navy Mine Rock, off the Naval Mine Depot; Bell Rock, in the vicinity of Bell Rock Light; and Pig Rock, above Bell Rock.

The river bottom varies from soft mud to hard sand and shell gravel. Over the oyster beds it ranges from stiff mud to gravel. In the deep channels soft mud predominates.

Geologically the York River Basin is similar to the basins of adjacent streams. It is typical for the sections lying in the coastal plain and the Piedmont Plateau. Most of the following brief description is summarized from the report of the United States Engineers (1930).

The deposits of the coastal plain, the area including all of the tidewater section, are chiefly soft, unconsolidated beds of sand, clay, loam, and marl. There are a few instances of the consolidation of the sand to sandstone and of the clay to shale. The sand and clay are filled with the shells of marine animals, an indication that at one time the region was covered by the sea.

The lands of the coastal plain are of the Eocene deposit and are among the most fertile in the State, particularly those along the Pamunkey. This superiority is due to the extensive marl deposits underlying them, appearing close to the surface along the borders of the streams. The lands of the Mattaponi rest on marl and blue clay, while those of the Pamunkey rest on the more fertilizing marl known as greensand. The Mattaponi marl beds contain shells, corals, and traces of phosphates, but do not reveal the greensand common on the Pamunkey.

The Piedmont Plateau portion, extending from the fall line to the foothills of the Blue Ridge, is sharply defined along its eastern border by the fall line where the rocks of the plateau pass beneath the nearly horizontal sediments of the coastal plain. The rocks of this area are the oldest in the State, ranging from pre-Cambrian to Silurian, and are largely crystalline masses, granites, gneisses, and schists occurring locally.

The topography of the country combined with many other factors, such as the preparation of virginland for agriculture, deforestation, climatic conditions, construction of city improvements, the development of roads, has an effect on the run-off of water. The stream flow of a river is, therefore, dependent on the precipitation and on all conditions determining the run-off of waters in its drainage basin.

Owing to the proximity of the ocean, the York River Basin receives a substantial share of precipitation falling along the Atlantic coast. According to the United States Engineers (1930), the average precipitation for the entire area amounts to 41.25 inches, varying from 40 to 45 inches. The area above West Point receives 41 inches. The snowfall varies from 8 inches at the coast to about 18 inches at the western edge of the watershed, the mean being 14.3 inches for the entire area. Highest rainfall occurs in June, July, and August, the maximum for the year coming in August. March, April, and May receive the next highest amount. The minimum rainfall occurs in November. The greatest run-off occurs during the winter, and the least during the summer.

According to the records published in the Water Supply Papers, United States Geological Survey, there are only two localities in the York watershed where discharges are measured. One station is located at Ashland, Va., on the South Anna River, the drainage area being 393 square miles, or 14.8 percent of the total, and the other at Doswell, Va., on the North Anna River, the drainage area being 439 square miles, or 16.5 percent of the total. Both rivers are tributaries of the Pamunkey, and the discharges have been measured at these localities from 1929 to date. During the period 1926 to 1928, discharges were measured at Vontay and Hewlett, Va., on the South and the North Anna Rivers, respectively. The results of the measurements at these stations give the flow of the Pamunkey River above the fall line. No data are available for the Mattaponi River.

Of more importance to a consideration of the rate of flow and discharge of water for the lower portion of the watershed is the hydrograph prepared by the United States Engineers (1930) and reproduced in figure 3. This hydrograph, based on precipitation records for the York River and adjacent streams and on mean monthly run-off records for adjacent streams, shows the average monthly flow of the York River at West Point for the 20-year period starting in 1907 and ending in 1928. The mean run-off into the York River at West Point was 2,263 second-feet. The maximum was 11,431 second-feet and the minimum about 300 second-feet.

TIDES AND CURRENTS

One of the causes of the cylic changes in the environment of organisms living in estuaries is the

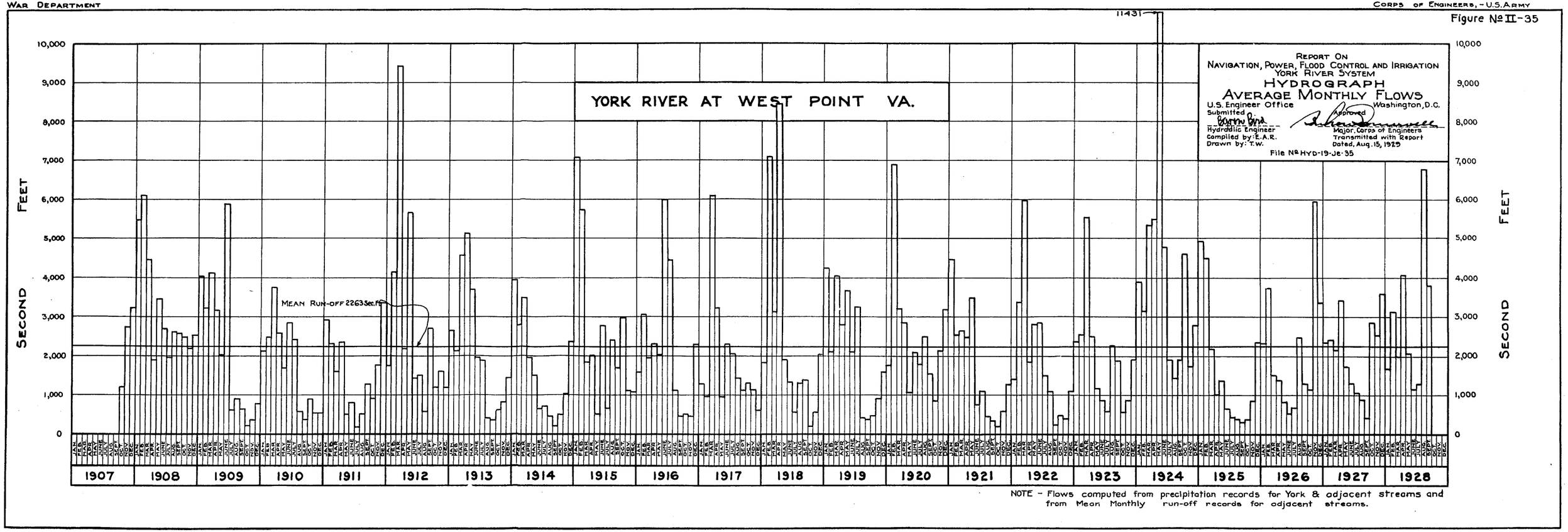

FIGURE 3.—Hydrograph of the York River at West Point. The average monthly flows were computed from precipitation records for the York River and adjacent streams and from mean monthly run-off records for adjacent streams. Reproduced from the Report of the United States Engineers [1929], War Department [1930].

rythmical motion of the tidal waters. In order to understand these changes it is necessary to consider what effects are brought about by this motion and how the sea and the fresh water moving down the river interact to vary the environmental conditions.

Tidal movement is of two types, vertical rise and fall and horizontal forward and backward movement, both forming parts of the same phenomenon resulting from the tidal forces of sun and moon. The horizontal movement of the tidal current generally has considerable velocity in entrances to bays and rivers. It continues in one direction for a period of about 6 hours and then reverses and flows in the opposite direction for the next period of about the same duration.

In rivers the tidal current is influenced by the nontidal movement of water. Generally speaking, the nontidal movement affects the rectilinear tidal current by making both the periods and velocities of flood and ebb unequal and by changing the time of slack water. It does not affect the times of flood and ebb strengths. The speed with which the particles of water move past any point depends upon the volume of water that must pass this point and the cross section of the channel at that point. From the product of time and the average velocity during the interval of time, the distance can be determined.

Observations of tides and currents in the York River and its tributaries have been made at various times from 1857 to 1928. The results of these surveys have been summarized by Haight, Finnegan, and Anderson (1930), who state (pp. 53–54):

> The observations show that the high water interval increases from 8.5 hours at York Spit Lighthouse to about 9 hours at Gloucester Point, and to about 10.8 hours at West Point. It is noted that the time of high water is earlier in the Mattaponi River than in the Pamunkey for equal distances from West Point. The duration of rise shows a slight decrease in value between York Spit Light and West Point. There is also a decrease in the duration of rise from West Point up the Mattaponi River. There is an apparent increase in the duration of rise in the Pamunkey River from 5.68 hours at West Point to 5.89 hours at Northbury Landing.
>
> The range in the York increases from about 2.2 feet at the entrance to about 2.5 feet at Gloucester Point and to about 2.8 feet at West Point. The range in the Mattaponi River increases from about 2.8 feet at West Point to about 3.9 feet at Walkerton. The range in the Pamunkey River increases from about 2.8 feet at West Point to about 3.3 feet at Northbury Landing. In the upper reaches of the latter two rivers the range decreases rapidly.

Observations of tide at West Point for 1 day in 1857 showed the high-water interval to be 10.23 hours. The duration of rise was found to be 5.81 hours. The low-water interval was 4.42 hours, and the mean range of tide 3.36 feet. For a period of 150 days in 1911–12 the high-water interval was found to be 10.79 hours, and the low-water interval 5.11 hours. The duration of rise was 5.68 hours. The mean range of tide was 2.82 feet. Observations for 3 days in 1918 showed the high-water interval to be 11.65 hours, the low-water interval 5.92 hours, the average duration of rise 5.73 hours, and the mean range of tide 3.65 feet.

From the data for 21 current stations, Haight et al. summarize results as follows (pp. 107-108):

> Two stations off Tue Point at the mouth of the river and a third about 3 miles above the mouth show current velocities at strength of slightly less than 1 knot. Observations in mid-channel between Gloucester Point and Yorktown show an average velocity of 1.4 knots at strength of flood and 1.8 knots at strength of ebb. Two stations nearby, one near each side of the channel, give strength velocities of about 1.2 knots for both flood and ebb in these locations. Velocities from three stations between Yorktown and West Point range from 1.1 to 1.4 knots for strength of flood and from 1.5 to 1.7 knots for strength of ebb.
>
> At the bridge over the Mattaponi River near West Point velocities of 1.3 knots for the flood and 1.4 knots for the ebb strengths were indicated by the observations. At a station below Mattaponi the flood and ebb strengths were 1.4 and 1.7 knots, respectively. At Walkerton the observed flood and ebb strengths were slightly less than 1 knot. At Aylett the current did not flood during 10 hours of observation, the maximum velocity being about 1 knot in an ebb direction.
>
> Flood and ebb strengths of 1.7 and 1.9 knots, respectively, were obtained from observations at the bridge over the Pamunkey River near West Point. Below White House one day of observations gave a flood velocity of 1.2 knots and an ebb velocity of 1 knot. Farther up the river about half way between White House and Bassett Ferry a similar series gave flood and ebb strengths of 0.5 knot and 1.3 knots respectively. At a station a short distance above Bassett Ferry during 7 hours of observation the current did not flood, the maximum ebb velocity being about 1 knot.
>
> Inspecting the time relations for the York River some roughness appears in the observational values, but from a general consideration of the results the following approximate relationships are derived. From the mouth of the river to Yorktown the strength of flood occurs about 1 hour before high water at Old Point Comfort. Above Yorktown the current becomes later, the strength of flood in the general vicinity of Ferry Point being simultaneous with high water at Old Point Comfort.
>
> Results of observations at the two bridges near West Point substantiated by observations near by, indicate that at the bridge over the Pamunkey River the current is 0.8 hour later than at the bridge over the Mattaponi River. Above West Point in the Mattaponi River the current becomes progressively later. At Walkerton, observations during one day show that strengths of flood occur almost 2½ hours after high water at Old Point Comfort or 3½ hours after the corresponding phase of the current at the mouth of the York River.
>
> Similarly the current becomes later in the Pamunkey River, observations at stations below White House and about half way

between White House and Bassett Ferry indicating strengths of flood apparently 2½ hours and 4 hours respectively after high water at Old Point Comfort.

In the York River the current and tide appear to advance up the river at about the same rate, each movement requiring about two hours to travel from the mouth of the river to West Point. Above West Point in the Mattaponi and Pamunkey Rivers the current becomes progressively earlier with respect to the tide.

SILTING

Deposition of silt in the tributaries of York River takes place principally at the time of floods. In the lower sections of these tributaries this process is expedited by the holding back of flood water by tidal action. Silting is also responsible for filling in the estuaries and gradual formation of mud flats and bars. The process is offset, however, by tidal or flood currents and by the sinking of the coast line.

Some studies of the silting of the upper York River estuary have been made by the United States Engineer Corps in the course of their work of maintaining the channel for navigation purposes. According to their reports, prior to 1880 there existed two bars obstructing navigation of the river for vessels of large draught. One of these was situated below West Point, and the other opposite Poropotank River. Both bars were formed over a period of many years and were composed principally of fine black sand, blue mud, and broken shells.

The still existing project for improvement of navigation in the York River, adopted by the River and Harbor Act of June 14, 1880, and modified in 1884 and 1887, provides for dredging through the bars a channel 22 feet deep at mean low water and 400 feet wide, and a basin of the same depth at the wharves at West Point on the Pamunkey River side. The project includes the construction of a dike on the right bank of the York River at West Point to assist in maintaining the channels.

The project was about 75 percent completed in 1899; the part not completed was the dredging of the channels to the full width of 400 feet, which was not considered necessary at that time. Subsequently, the amount of navigation on the York River has not justified the completion of the project. In 1899 a pile and timber dike, 10,412 feet in length, was built parallel to the right shore of the river, a short distance below West Point. The dike is now in poor condition although still of value in channel rectification. Dredging on the project has been confined to the bar below West Point, the turning basin at the West Point wharves in the Pamunkey River, and the bar at the mouth of Poropotank River.

Poropotank Bar has been dredged only once, from December 28, 1880, to March 31, 1881. An examination made in January 1890 of the channel at this bar disclosed a deposit of between 2 and 3 feet accumulated during the period of 9 years. This rate of silting was much less rapid than that observed at West Point. Examinations of the controlling depths at Poropotank Bar, made in July 1905, November 1927, March 1929, November 1934, and June 1936, showed that shoaling on the bar took place only during the first few years after dredging. From that time until the present the bar has not shoaled to any appreciable extent.

To meet the specifications of the project and to maintain the desired depth, extensive dredging has been carried out at the West Point Bar and at the turning basin. The rate of silting in this area was so great that in 1 year (1890) from 2 to 3 feet of sediment accumulated in the bar. Construction of the dike in 1893–94 aided in transferring the silting action farther down stream, and except for the dredging in 1901, all subsequent maintenance operations have been restricted to the removal of the material from the turning basin at West Point.

A controlling depth of at least 20 feet was reported after dredging in 1901. The controlling depths at the channel reported after this last dredging are:

Year:	*Feet*
1910	18–21
1927	19
1929	21.5
1934	21
1936	19.5

During the fall of 1938 an investigation of sedimentation in the York River estuary was made by the Section of Sedimentation Studies, Division of Research, Soil Conservation Service, of the United States Department of Agriculture. The preliminary report (Brown, Seavy, and Rittenhouse, 1939) deals chiefly with the comparative survey data and does not consider the character of sediment on the bottom or discuss the causative factors of sedimentation.

The method adopted in this study consisted in comparing the water depths in 1938 with water depths in 1857, 1911, and 1918, as shown on United States Coast and Geodetic Survey charts. This comparison was made within the 20 upper miles of the York River along the 13 ranges across the estuary, and the amount of fill, or scour, was computed.

From 1857 to 1911 the cumulative volume of sediment deposited was 5,591 acre-feet as com-

pared with 15,293 acre-feet accumulated between 1911 and 1938. Thus, for the first period of 57 years there was an accumulation of 104 acre-feet per year. For the following 27 years the net accumulation was 566 acre-feet per year. The water volume for this segment of the river was computed to be 206,896 acre-feet in 1938. In 1911 it was 222,189 acre-feet, and in 1857 it was 227,780 acre-feet. The annual loss of water volume was at the rate of 0.05 percent per year from 1857 to 1911 and 0.25 percent per year from 1911 to 1938.

From 1857 to 1911 there were two main areas of heaviest silt accumulation, one at the head of the estuary between West Point and Fillbates Creek, and one in the upper middle estuary between Ware Creek and lower Purtan Bay. There was an area of scour at Bell Rock separating them. A larger area of scour was below Purtan Bay. During the period from 1911 to 1938 there were also two areas of fill and two of scour. The point of greater accumulation in this period, however, had moved downstream below lower Purtan Bay along Capahosic almost to Jones Creek. Also during this period scour occurred in the area below West Point where fill had occurred from 1857 to 1911. The annual rate of accumulation during the latter 27-year period was more than five times the rate during the preceding 57-year period.

Comparison made between the two periods of different durations raises a question of the significance of the difference in the rate of sedimentation computed by the investigators. They qualify, however, their conclusion by stating (p. 9), "the filling has not been a continuous process between these dates" (1857, 1911, 1938). "There appears, however, to be some orderly relation of scour and fill at the various ranges."

The selection of the above-mentioned dates was governed by the availability of three sets of hydrographic charts of the United States Coast and Geodetic Survey used for comparison. It is fortunate, however, that the second period (1911–38) almost coincides with the operations of the pulp mill, which was organized in 1913.

The authors' conclusion regarding the "downstream migration of the locus of most active sediment deposition" is of particular interest in the present investigation, for it throws some light on a probable distribution of a pulp-mill pollutant in the river. Discussion of this question is given on page 171.

POLLUTION

The York River receives domestic sewage and industrial waste, nearly all of which are emptied at the head of the river at West Point, Va.

Previous to 1935 the greater part of the sewage from the city of Williamsburg, Va., was discharged untreated into the headwaters of Queens Creek, which enters the York River from the right side about 8 miles above Yorktown. As a result of this, the creek was highly polluted and restrictions were made by the Virginia Department of Health on the sale of shellfish from the creek. In the early part of 1935, the city of Williamsburg installed two sewage pump stations and a plant for complete treatment of the sewage from the city. Since that time all sewage from the city is being discharged into College Creek, a tributary of the James River. On April 8, 1935, after shoreline surveys indicated that all unsanitary conditions had been corrected, and bacteriological samples showed safe water conditions, the restriction was lifted and Queens Creek was no longer classified as a restricted shellfish area.

At the confluence of the Pamunkey and Mattaponi Rivers the York River receives raw, untreated sewage from the city of West Point. Because of this pollution the Virginia Department of Health prohibits the sale of shellfish taken from the upper York River. This order, issued October 5, 1929, outlines the restricted area as "that portion of the York River lying above a line drawn in a northeasterly direction from the point of land at Mount Folly through Red Spar Buoy No. 10 to the shore near Roane; that portion of the Mattaponi and Pamunkey Rivers lying below a line drawn at right angles to the King William County shores two miles from their points of entrance into the York River." The lower limit of this area[2] is shown in figure 2.

The only important source of industrial pollution of the York River arises from the effluents of a pulp and paper mill located about 1½ miles upstream from the head of the York River on the outskirts of the city of West Point. This mill was established in 1913 as the Chesapeake Pulp & Paper Co. and was reorganized in 1918 as the Chesapeake Corp. In 1930 it absorbed the plant of the Albemarle-Chesapeake Co. which converted the pulp to paper and paperboard. At present the finished products of the mill are pulp and unbleached paperboard used in the

[2] In 1942–45, the sewage pollution in the York River greatly increased owing to the establishment of military camps. Consequently, the restricted area has been extended and covers at present a large portion of the oyster bottoms in the lower part of the river.

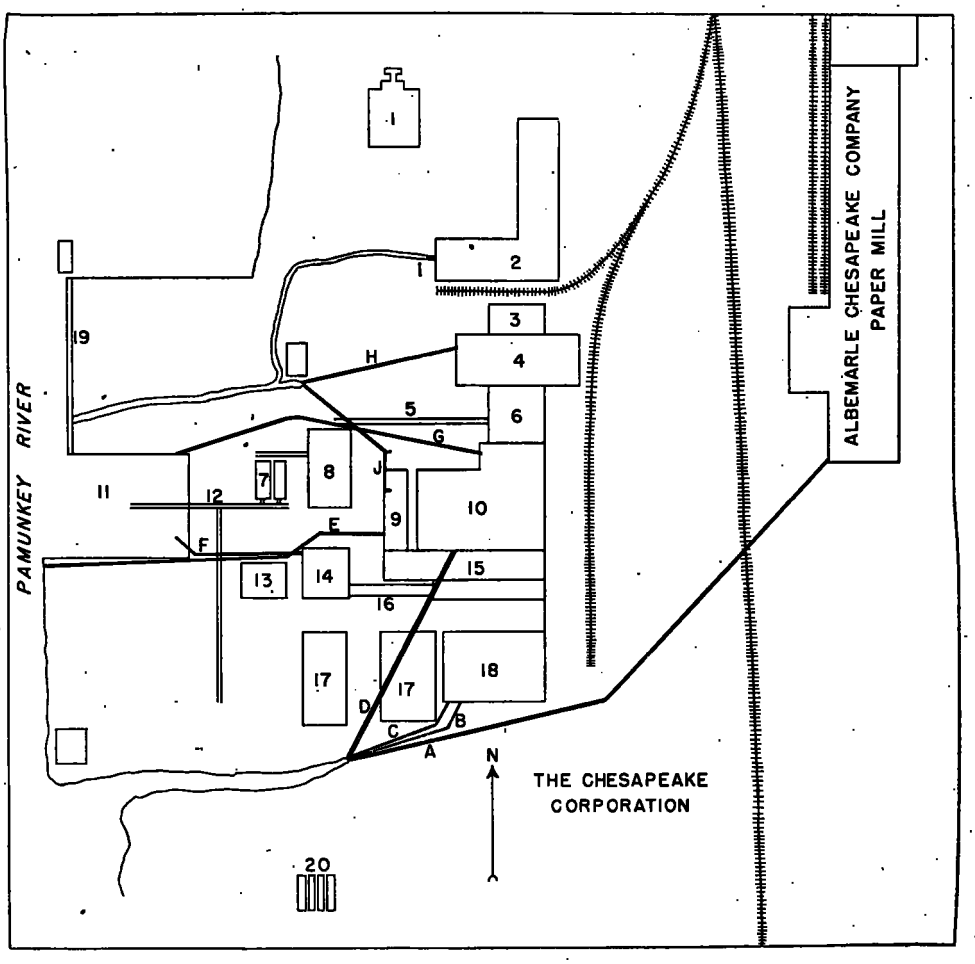

FIGURE 4.—General arrangement of buildings and sewer outlets of the Chesapeake Corporation pulp mill and the Albemarle Chesapeake Company paper mill in January 1936. The buildings are numbered from 1 to 19, and the sewer outlets are lettered from A to J, inclusive.

Buildings

1. General office.
2. Old board mill.
3. Screening building.
4. Diffuser building.
5. Chip conveyor.
6. Digester building.
7. Barking drums.
8. Chipper house.
9. Evaporator building.
10. Recovery room.
11. Lighter slip.
12. Log conveyor.
13. Bark boiler.
14. Slacker house.
15. Causticizing building.
16. Kiln.
17. Steel building.
18. Power house.
19. Wharf.

Sewers

A. 15-inch sewer from paper mill.
B. 14-inch sewer for drips, leaks, cooling water, etc., from power house.
C. 4-inch blow-down line from power house.
D. 39-inch sewer from recovery room.
E. 14-inch salt water return from vacuum jet.
F. 10-inch sewer from slacker house.
G. 2½-inch blow-down line from boiler.
H. 30-inch sewer from diffuser building.
I. Small drain from old board mill.
J. 15-inch sewer from evaporator building.

manufacture of containers. The combined plants have been increasing their facilities rapidly and the production has kept pace with the expansion.

Data on annual production, supplied by the Chesapeake Corp., are shown in table 1. There has been a steady increase for each year except 1930 and 1934. Starting in 1930, the increase in production has been much more rapid. The drop in 1934 was compensated by an increase in 1935 sufficient to bring the production figure back in line with the increases for other years.

The processing of pulp and paper requires large quantities of water, which this plant obtains from deep wells. Information furnished by the plant chemist gave the approximate quantity of water used by the Chesapeake Corp. in 1936 as 9,500 gallons per ton of pulp. In comparison with other mills this is a surprisingly small amount (Hagenauer 1937). In 1919 the plant pumps were said to have a capacity of 600 gallons per minute, or nearly a million gallons daily. At present the maximum amount of water delivered per minute by the pumps is 4,510 gallons, and daily delivery has reached 4,874,400 gallons.

TABLE 1.—*Annual production of pulp by the Chesapeake Corp., West Point, Va.*

Year	Tons	Year	Tons	Year	Tons	Year	Tons
1919	4, 884	1924	19, 714	1929	37, 090	1934	71, 641
1920	10, 862	1925	23, 193	1930	36, 779	1935	86, 844
1921	13, 870	1926	25, 883	1931	50, 990	1936	95, 075
1922	15, 127	1927	29, 910	1932	61, 608	1937	101, 004
1923	18, 064	1928	34, 808	1933	72, 666		

Although the mill uses every effort to reduce to a minimum the water needed in both the washing of pulp and the making of paper, much of the process water finally reaches a condition where it is no longer reusable and is discharged into the sewers and released into the river.

An approximate lay-out of the buildings and sewers of the plant (fig. 4), obtained from an official of the mill, in January 1936, shows 10 sewers discharging into the Pamunkey River directly or through ditches which flow into this river. The sewer lines have been labeled alphabetically in order of their occurrence from south to north. At that time the estimated flow of the main sewers was as follows: sewer *A*, 200 gallons per minute; sewer *D*, 150 gallons per minute; and sewers *J* and *H*, 1,200 gallons per minute. Thus, the total amount of mill water discharged at that time into the river was 1,550 gallons per minute, or 2,232,000 gallons a day.

HISTORY OF THE YORK RIVER OYSTER INDUSTRY

The history of the oyster industry of the York River was compiled from a variety of sources. Records of oyster dealers handling York River oysters were examined and interviews were held with 30 oyster planters of the river and with State oyster inspectors and others associated with the industry.

In former years the upper York River produced oysters of excellent quality. This opinion is substantiated by the fact that in 1904 A. F. Smither, one of the oyster packers at West Point, was awarded a silver medal for the excellency of the oysters grown in the upper part of the York River and exhibited at the Louisiana Purchase Exposition in St. Louis, Mo.

Further evidence of the good quality of the oysters produced in the upper York River in earlier years and their subsequent decline is found in the books of the local oyster dealers. Their records showing amount of business, prices of shucked oysters, and other data reveal a marked decrease in the quantities of oysters handled and the fall in prices resulting from poor quality. It seems that the downward trend, which began in 1916–18, has continued until the present time (1939).

A typical example of the falling off in the industry can be found in the records of A. L. Van Name, who kept a detailed account of his operations. His grounds, covering 200 acres, are located about 9 miles below West Point. For the first 13 years, 1901–13, the total profit of this company was $38,577.85, averaging $2,967.33, annually. During the following 23 years, from 1914 to 1936, the total profit was only $11,181.30, or $486.14 a year. Because of the small returns, or in many cases actual loss, the planting of oysters was discontinued by this company in 1931.

Complete information as to the number of bushels of oysters marketed from the York River from year to year is impossible to obtain. A decline, however, can be seen from the records of oysters bought by M. D. Shields of Dandy, Va., who operated two 75-foot oyster boats each holding from 400 to 500 bushels. Figure 5 shows the number of bushels of upper York River oysters bought by him by years from 1920 to 1935. This decline resulted from the inability of this dealer to obtain good marketable oysters from this area.

The condition of the oyster industry in the upper York River can be readily understood when it is

realized that one of the four oyster shucking houses at West Point was forced out of business in 1920, another in 1925, another went into bankruptcy in the spring of 1937, and the fourth ran its business at a loss until 1938. In all cases, the chief cause of failure was the refusal of the shippers and dealers to buy the oysters because of poor quality.

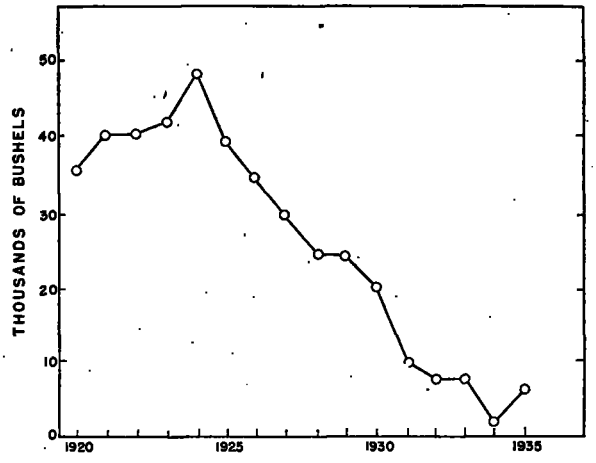

FIGURE 5.—The number of bushels of oysters bought in the upper York River by M. D. Shields from 1920 to 1935, inclusive.

Information from the York River oyster planters, obtained through interviews and correspondence, is summarized in table 2, in which the lessees are arranged in geographical order, starting from West Point. One can notice that the line of demarcation between the sections producing oysters of good quality and those producing oysters of inferior quality can be roughly drawn about 15 miles below West Point, near Claybank. The year when poor oysters were first noticed by the planters is given in column 7. In case no definite answer was received to this question, the statement of the planter is quoted in the footnote.

Because most of the planters kept meager records of oysters handled, and because of the diversified methods of transporting them to market, it is impossible to trace the fluctuations in the total production of the river over a period of two or three decades. Several of the dealers and State oyster inspectors, when asked to give an approximate estimate of the quantity of seed oysters planted and the vol-

TABLE 2.—*Summary of information obtained from the York River oystermen through interviews and questionnaires*

Miles below West Point	Side of river	Lessee	Acres	Character of bottom	Bushels planted per acre	Year bad oysters first noticed	Last planting
2	East	Richardson, G. W	40	Broken [1]	1,000	1917–18	1923
2	West	Towsend, R	4½	Hard	600–800	1916	1923
8	East	Roane, C	149	Soft	1,400	1916	1923
8	do	Allmond, J	17½	do	1,246	1916–17	1926
9	do	Van Name, A	200	do	600–800	1915–16	1931
10	do	Eastwood, E. C	22	Stiff	800	1925	1928
10	West	do	8	do	800	1925	1928
11	East	Scanlan, J. E	175	do	600	1920	1931
11	West	do	156	Soft	800	1930	1931
12	East	Twyford, F. P	38	Stiff		1920	1931
12	West	Twyford, J. H	40	Soft	1,210	1928	1931
13	East	Allmond, J. M	15	Broken	1,246	1929–30	1931
13	do	Allmond, W. W	15	Hard	1,452	1917	1931
13	West	Allmond, W	60	Soft	1,452	1917	1931
13	East	Eastwood, E. C	24	Stiff	800	1928	1928
13	West	Tuttle, E. T	18	Soft	1,452	(2)	1930
14	East	Twyford, J. H	26¼	Stiff	1,210	1928	1931
14	do	Groh, Louis	120	Broken	1,500	1926–27	1927
14	do	Marnix, C. C	15½	Stiff	522	1928	1927
14	West	do	21	do	1,452	1928	1927
14	East	Puller, R. F	18	do	1,452	1921–23	1927
14	West	do	48	do	1,452	1921–23	1929–30
14	East	Stubblefield, R	30		700	1920	1929–30
14	West	do	12		1,000	1920	
16	do	Newman, A. H	41	Stiff	826	[3] 1918	1929–30
16	do	Townsend, R	53	do	600–800	(4)	(5)
16, 17	do	Powers, D. A	130	do	1,000	(6)	(5)
17	do	Maynard, E. W; Hansford, J. D	85	Soft	1,000	1917–18	(5)
21	East	Wilburn, R. L	12	Stiff	1,000	(7)	(5)
21	do	Diggs, W. H				(8)	(5)
21	do	Carmine, R. S	31	Stiff	1,000	1935	(5)
23	do	Tillage, A. H	25	Hard	500–1,000	(8)	(5)
23	do	Tillage, J. C	3	Soft	500	(8)	(5)
26	do	Blake, T. J	120	Broken	500	(8)	(5)
28	do	Tillage, A. H	75	Hard	500–1,000	(8)	(5)
26	do	Tillage, J. C	17	do	500	(8)	(5)

[1] Of various degrees of consistency.
[2] "Not many years ago."
[3] Freeze.
[4] Not affected.
[5] Still planting.
[6] "When pulp mill started on large scale."
[7] "Weakened in last few years."
[8] No change.

ume of oysters marketed, agreed that, before 1928, the planting was in excess of 200,000 bushels annually and that the annual production of market oysters was about 400,000 bushels. This activity necessitated the employment of about 500 tongers and the use of about 30 locally owned boats to plant seed oysters and to carry the oysters to market. In more recent years only about 50,000 bushels of oysters have been marketed annually.

An early method of oyster culture in the York River consisted of transplanting oysters from the lower and middle sections of the river to beds extending to about 5 miles below West Point. In recent years the process has been reversed, not because of the closing of restricted oyster grounds of the upper York River by the Health Department, but because of the failure of oysters to grow and fatten in that section. Although the marketability of oysters from the upper and middle river is subject to great seasonal variations, it can be said that as a general rule oysters from the upper and middle sections of the river have to be moved to the lower York River, or out of the river entirely, in order to obtain a satisfactory marketable product.

Official records in the office of the Virginia Commission of Fisheries show that in June 1937 there were 5,971.41 acres of oyster bottom under lease in the York River. This figure has fluctuated from year to year as the parcels of bottom have been given up or leased again. As all of the leased parcels probably are not cultivated every year, the total acreage of leased bottoms does not necessarily represent the total number of acres under cultivation. The bottoms cultivated by the oystermen who consented to supply information regarding their business cover 1,864.75 acres, or about one-third of the acreage under lease. They represent a good proportion of the bottoms in the sections of the river seriously affected by pollution.

PHYSICAL AND CHEMICAL CONDITIONS OF THE WATERS OF THE YORK AND PIANKATANK RIVERS

No study of the biology of any waters would be complete without a consideration of the physical and chemical conditions under which the organisms are living. Physical and chemical factors of the environment may have either direct effect on living forms by controlling their growth and propagation or they may exert indirect, but nevertheless important, action by influencing the abundance, distribution, and sequence of changes in the populations of microscopic organisms upon which other forms subsist.

Reproduction and growth of the oyster or of any other organism which obtains its food by filtering water are often limited by the deficiency in the type of food needed by them. Thus, the productive capacity of an oyster bottom is determined by the availability of the microorganisms necessary to support the life of the oyster during its larval and adult stage. Observations of various investigators indicate that diatoms, dinoflagellates, and other groups constituting phytoplankton, comprise the principal items of an oyster's diet. It is possible that bacteria also have a part in the feeding of oysters, although convincing evidence on the subject is still lacking. The abundance of phytoplankton, estimated indirectly by Harvey's method of pigment units, can be accepted only as a more or less general indication of the abundance or scarcity of oyster food in water, for the nutritive value of various forms comprising the phytoplankton has not yet been ascertained.

Although most of the studies in this paper deal with conditions of the York River, a number of parallel observations were made in the Piankatank River. Situated a short distance north of the York River, the Piankatank is also one of the tributaries of the Chesapeake Bay. With respect to the character of the bottom, water conditions, tides, and other hydrographical features, it resembles the York River, but it is not contaminated by domestic or industrial pollution. The river is known to produce excellent oysters. For these reasons, observations made in it are considered as controls for those carried out in the York River.

A number of sampling stations for physical, chemical, and biological observations were established at rather regular distances from the mouth of the York River to localities above West Point in the Pamunkey and Mattaponi Rivers, and at two localities in the Piankatank River, one in the lower portion and one in the upper. Many of these stations were also used for experimental oyster planting and for regular examination of the oysters. Locations of the stations are shown in figure 2 and described in table 3. Other substations were established for special needs and are described in the text as discussed.

TABLE 3.—*Location and character of hydrographic stations in the York and Piankatank Rivers*

Station	Location	Depth of water in feet	Character of bottom
	YORK RIVER		
	Yorktown, Steamboat Dock	14	Hard, sand.
	Naval Mine Depot Dock	12	Do.
	West Point, Bruce Memorial Bridge.		Soft, mud.
5	Off Allmondsville	3.9	Medium, stiff mud and shell.
6	Below Scimmino Creek	5.2	Do.
8	Bell Rock Lighthouse	13.6	Hard, shell, oyster rock.
9	Middle Ground below West Point.	12.4	Hard, sand with little mud.
14	Off Carmines Islands	8.3	Hard, mud and sand.
15	Above Queens Creek	3.4	Medium, mud and shell.
16	Off Roanes Point	4.2	Soft, stiff mud.
17	Off Ware Creek	3.9	Soft, mud, little shell.
18	Pamunkey River above West Point.	29.5	Soft, mud.
19	Mattaponi River above West Point.	15.0	Do.
20	Off Sandbox, above Bull Creek	10.5	Hard, sand.
22	Inside Purtan Bay	4.1	Medium, stiff mud and shell.
23	Above Claybank	4.6	Medium, mud and sand, shell.
	PIANKATANK RIVER		
53	Off Ferry Creek	7.3	Medium, stiff mud, shell.
55	Off Iron Point	4.2	Hard, sand and shell.

OBSERVATIONS ON CURRENTS

Although the tide tables issued by the Coast and Geodetic Survey and the paper by Haight, Finnegan, and Anderson (1930) give essential information regarding the tides and surface currents in the York River, it was considered necessary to obtain more detailed knowledge regarding the velocity of currents at different depths and at different stages of the tide. These data were particularly needed for evaluating the river discharge (the excess of the discharge during the entire ebb period over the entire flood period) and for computing the velocity of the resultant current of the river.

For the observation of tides a station was established on the Texas Oil Co.'s dock on the Mattaponi River at West Point. According to the specifications of the United States Coast and Geodetic Survey (1935), a tide house was constructed over a wooden float-well formed by joining four 2-inch by 14-inch planks into a box. After the establishment of bench marks, a standard automatic tide gage, loaned by the Coast and Geodetic Survey, was installed and put into operation. Observations were continued from August 25, 1936 to May 5, 1937.

Measurements of the currents of the York River were made during the fall, winter, and spring of 1936–37 as follows: August 10–11; September 16–17 and 23–26; October 28–30; November 18–20; December 17–19; January 18–20; February 8–10; March 8–10; April 13–14 and 29. The stations occupied were arranged in a line across the river at Purtan Island (fig. 2) so that a relatively complete cross section of the river was made. This section was chosen because of the straightness of the channel at that point. Depths of water on this line were determined by soundings made at regular intervals and the position determined by angles at each sounding. The contour of the bottom at this section is shown in figure 6. Station 1 was located in the deepest water of the channel and was occupied and observations were made continuously whenever any measurements of flow were determined at any station. This served as a reference station for stations 2, 3, 4, and 4A, where observations were made for shorter periods of time.

The procedure of observations was patterned after that described by Zeskind (1926). The boat was brought up on station and anchored from the bow by as short a cable as was practical. It was found inconvenient to anchor fore and aft, and for this reason position angles were determined by sextant each hour as the boat swung with the tide. The Price current meter suspended by the electric cable and weighted to insure a vertical position of the cable, was lowered to a level of two-tenths of the total depth. The revolutions were then counted for 1 minute with the use of a stop watch. Following this, the meter was lowered to five-tenths of the total depth and observations were made. After this the meter was again lowered and observations were made at eight-tenths of the total depth. A second set of observations was made at eight-tenths, five-tenths, and two-tenths of the total depth as the meter was raised.

Immediately after the meter readings were completed, observations were made of the current velocity by using the current pole floating vertically in the water. The graduated line was allowed to run out for 1 minute and the distance the pole traveled recorded. The direction of the pole from the boat was then determined either by a pelorus or by sextant angles. The wind velocity and direction as well as the ship's head by compass were also noted.

These observations were continued every half hour as long as the station was occupied. The time varied from 13 hours to 3 days, a 13-hour complete tidal cycle being the minimum period of observation. With interruptions, the current meter studies were conducted between August 1936 and April 1937.

The results of the measurements of current velocities at each station are shown in table 4. All of the

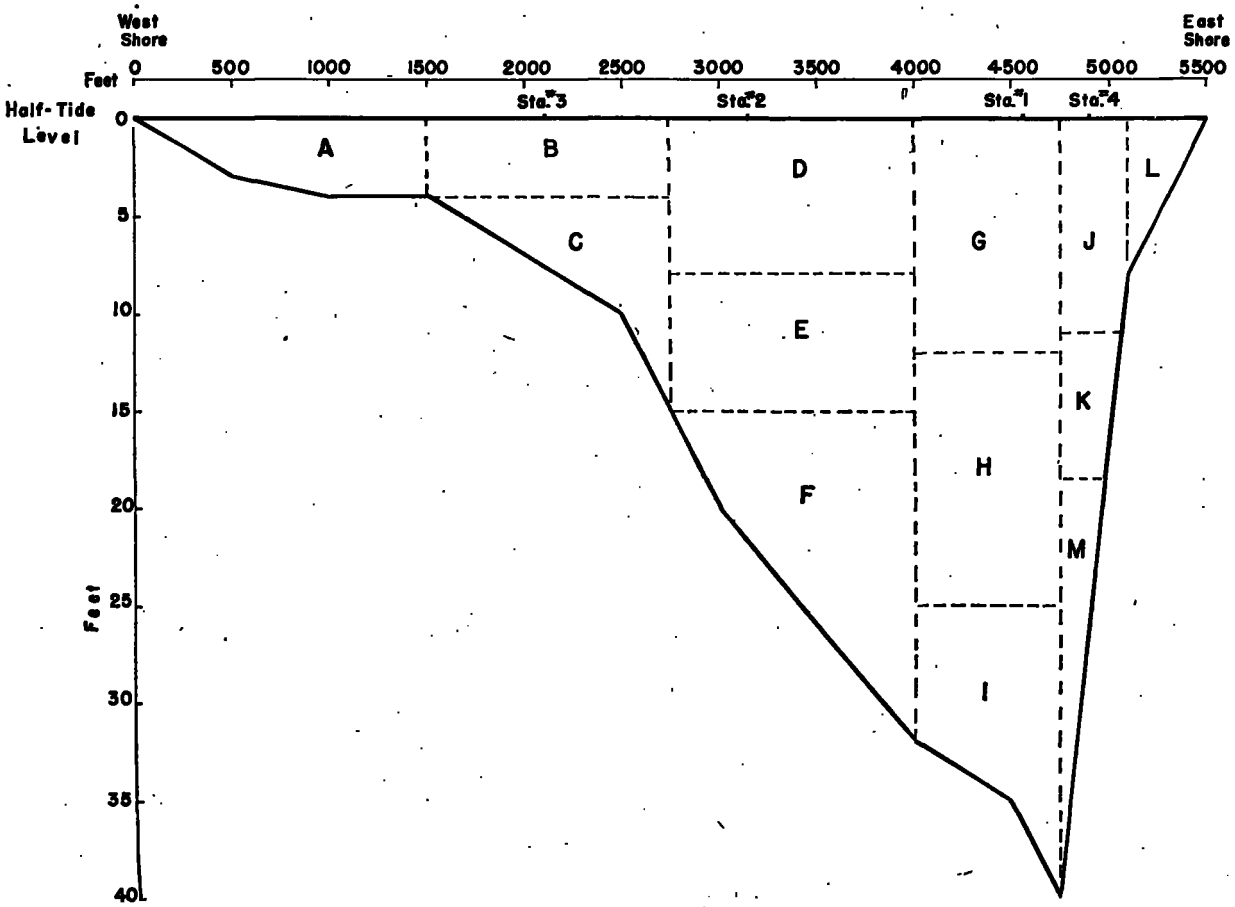

FIGURE 6.—Approximate cross-section of York River (Purtan Island) for determination of river flow based on current observations made in 1936–37. The depths and widths are approximate values derived from data obtained from the United States Coast and Geodetic Survey hydrographic sheet 3311 showing the results of a survey in this area in 1911. The approximate area of each section in square feet follows: A—4,500; B—5,000; C—5,125; D—10,000; E—8,750; F—11,625; G—9,000; H—9,750; I—7,375; J—3,750; K—2,130; L—1,600; M—2,688.

data were analyzed by the United States Coast and Geodetic Survey and summarized as follows:

Staff readings corresponding to the different local tide planes as determined by comparison with the standard station at the Naval Operating Base, Hampton Roads, showed 4.57 feet at mean high water, 3.07 feet at half-tide level, and 1.57 feet at mean low water. The mean range of tide was 3.0 feet. High waters occur, on the average, 1.86 hours later than at the Naval Operating Base, and low waters 2.32 hours later. The average duration of rise was 5.62 hours, and the average duration of fall 6.80 hours.

One of the purposes of current-meter observations at the section of the York River at Purtan Bay was to obtain estimates of the total flow at flood and ebb periods. These data can be computed if the cross-sectional area and the changes in the velocity of current at various depths across the river during various stages of tide are known. To aid in the computation, the entire cross section of the river was divided into several small sections (A to M, fig. 6), the limits of which are outlined wholly or in part by dashes. The area of each small section is indicated in the figure. The depths and widths shown in this diagram represent approximate values derived from data obtained from United States Coast and Geodetic Survey hydrographic sheets 3311 showing the results of a survey made in 1911. The upper limit represents the half-tide level of the river. On the basis of these data, the cross-sectional area of the river at this point was found to be equal to 81,293 square feet at half-tide level. In 1938 at our request, G. L. Evans, a surveyor of the Chesapeake Corp., determined the width of the river at Purtan Bay and made a series of careful soundings. Computed on the basis

TABLE 4.—*Current measurements in the York River in 1936 and 1937.*

[Referred to times of predicted tides at Hampton Roads, Va.]

Station No.	Date	Length of series	Method of observation	Average depth	Current intervals: Slack before flood	Current intervals: Strength of flood	Current intervals: Slack before ebb	Current intervals: Strength of ebb	Observed velocity: Flood	Observed velocity: Ebb	Correction factor	Corrected velocity: Flood	Corrected velocity: Ebb	Duration: Flood	Duration: Ebb	Resultant for nontidal current
	1936	*Days*		*Feet*	*HW+*	*HW+*	*LW+*	*LW+*	*Knots*	*Knots*		*Knots*	*Knots*	*Hours*	*Hours*	*Knots*
1	Aug. 10 to 11	1.0	Meter	4 to 7	−3.30	−0.30	−3.95	−1.50	1.20	0.85	1.10	1.30	0.95	5.69	6.73	−0.06
	Sept. 16 to 17	1.0	do	7	−2.80	−0.30	−3.45	+0.05	1.10	1.30	0.96	1.05	1.25	5.69	6.73	+0.13
	Sept. 23 to 26	3.0	do	7	−2.90	−0.07	−3.66	+0.06	1.35	1.18	1.43	1.89	1.72	5.58	6.84	+0.03
	Oct. 28 to 30	2.0	do	7	−3.12	−0.40	−3.60	+0.02	1.85	1.85	0.75	1.39	1.39	5.86	6.56	+0.07
	Nov. 18 to 20	2.0	do	7	−3.12	+0.50	−2.78	+0.38	1.40	1.48	1.17	1.64	1.72	6.68	5.74	−0.04
	Dec. 17 to 19	2.0	do	7	−2.90	+0.02	−3.05	−0.30	1.48	1.50	1.03	1.52	1.54	6.19	6.23	+0.01
	1937															
	Jan. 18 to 20	2.0	do	7	−2.85	−0.17	−3.90	−0.25	1.70	1.65	1.01	1.72	1.67	5.29	7.13	+0.14
	Feb. 8 to 10	1.75	do	7	−2.70	+0.48	−3.40	+0.03	1.72	1.97	1.01	1.74	1.99	5.64	6.78	+0.19
	Mar. 8 to 10	2.0	do	7	−3.07	+0.35	−3.22	−0.22	1.60	1.78	1.10	1.77	1.95	6.19	6.23	+0.06
	Apr. 13 to 14	1.5	do	7	−3.27	−0.43	−3.67	+0.23	1.97	1.80	0.77	1.54	1.37	5.94	6.48	0.00
	Apr. 29	0.5	do	7	−2.70	+0.20	−3.90	−0.50	0.80	1.60	1.16	0.99	1.79	5.14	7.28	+0.39
	1936															
1	Aug. 10 to 11	1.0	do	14 to 16	−3.75	−0.10	−3.80	−0.95	1.20	0.95	1.10	1.31	1.06	6.29	6.13	−0.09
	Sept. 16 to 17	1.0	do	18	−3.00	−0.40	−3.30	−0.20	0.80	0.90	0.94	0.75	0.85	6.04	6.38	+0.05
	Sept. 23 to 26	3.0	do	18	−2.93	−0.10	−3.60	0.00	1.38	1.10	1.43	1.90	1.62	5.67	6.75	−0.02
	Oct. 28 to 30	2.0	do	18	−3.12	−0.30	−3.42	+0.28	1.88	1.68	0.75	1.44	1.24	6.04	6.38	−0.03
	Nov. 18 to 20	2.0	do	18	−3.30	+0.30	−2.75	+0.42	1.45	1.28	1.17	1.67	1.50	6.89	5.53	−0.15
	Dec. 17 to 19	2.0	do	18	−3.60	−0.15	−2.95	−0.12	1.68	1.35	1.03	1.73	1.40	6.99	5.43	−0.23
	1937															
	Jan. 18 to 20	2.0	do	18	−3.22	−0.43	−3.92	−0.55	1.80	1.35	1.01	1.82	1.37	5.64	6.78	−0.05
	Feb. 8 to 10	1.75	do	18	−3.03	−0.25	−3.68	−0.43	1.82	1.63	1.01	1.84	1.65	5.69	6.73	+0.03
	Mar. 8 to 10	2.0	do	18	−3.40	−0.58	−3.38	−0.20	1.65	1.60	1.10	1.81	1.76	6.36	6.06	−0.04
	Apr. 13 to 14	1.5	do	18	−3.30	−0.33	−3.73	−0.23	2.03	1.93	0.77	1.57	1.47	5.91	6.51	+0.03
	Apr. 29	0.5	do	18	−3.50	0.00	−4.00	−0.70	1.50	1.60	1.16	1.75	1.85	5.84	6.58	+0.09
	1936															
1	Aug. 10 to 11	1.0	do	16 to 26	−3.75	−0.55	−3.65	−0.85	0.85	0.75	1.10	0.93	0.83	6.44	5.98	−0.05
	Sept. 16 to 17	1.0	do	29	−3.10	−0.40	−3.53	−0.80	0.70	0.90	0.94	0.65	0.85	6.09	6.33	+0.07
	Sept. 23 to 26	3.0	do	30	−2.86	−0.30	−3.66	−0.44	1.37	0.94	1.43	1.87	1.44	5.54	6.88	−0.06
	Oct. 28 to 30	2.0	do	28	−3.20	−0.05	−3.45	+0.30	1.78	1.45	0.75	1.38	1.05	6.09	6.33	−0.09
	Nov. 18 to 20	2.0	do	30	−3.42	−0.07	−2.78	+0.35	1.20	1.00	1.17	1.39	1.19	6.98	5.44	−0.15
	Dec. 17 to 19	2.0	do	28	−3.63	−0.35	−3.08	−0.25	1.22	1.08	1.03	1.25	1.11	6.89	5.53	−0.12
	1937															
	Jan. 18 to 20	2.0	do	28	−3.82	−0.60	−3.92	−0.40	1.67	1.02	1.01	1.68	1.03	6.24	6.18	−0.21
	Feb. 8 to 10	1.75	do	30	−3.20	−0.30	−4.02	−0.10	1.32	1.27	1.01	1.33	1.28	5.52	6.90	+0.08
	Mar. 8 to 10	2.0	do	28	−3.68	−0.55	−3.72	−0.40	1.12	0.98	1.10	1.22	1.08	6.30	6.12	−0.05
	Apr. 13 to 14	1.5	do	29	−3.50	−0.40	−3.67	−0.60	1.50	1.33	0.77	1.17	1.00	6.17	6.25	−0.05
	Apr. 29	0.5	do	29	−4.15	−0.90	−3.90	−0.09	1.10	1.40	1.16	1.30	1.60	6.59	5.83	+0.05
	1936															
2	Sept. 24	0.5	do	5	−3.40	−1.00	−4.10	+0.20	1.20	1.20	1.56	1.87	1.87	5.64	6.78	+0.07
	Oct. 28	0.5	do	4	−2.80	−0.60	−3.70	−0.10	1.60	2.10	0.81	1.25	1.75	5.44	6.98	+0.31
	Nov. 18 to 19	0.5	do	5	−3.10	+0.20	−3.30	−0.10	1.00	1.80	1.16	1.22	2.02	6.14	6.28	+0.26
	Dec. 17	0.5	do	4	−3.50	−0.20	−4.30	−0.90	1.00	2.00	1.02	1.03	2.03	5.54	6.88	+0.42
	1937															
	Feb. 10	0.5	do	5	−2.80	+0.30	−3.40	−0.20	1.60	2.00	0.91	1.44	1.84	5.74	6.68	+0.21
	Mar. 9	0.5	do	5	−2.70	−0.10	------	+0.30	1.40	2.30	1.14	1.66	2.56	------	------	------
	Apr. 13	0.5	do	4	−3.20	−1.00	−3.50	−0.30	2.10	2.10	0.75	1.58	1.58	6.04	6.38	+0.04
	1936															
2	Sept. 24	0.5	do	12	−3.40	−0.60	−3.90	+0.10	1.20	0.90	1.56	1.79	1.49	5.84	6.58	−0.06
	Oct. 28	0.5	do	10	−2.70	−0.40	−3.65	+0.10	1.40	1.60	0.81	1.12	1.32	5.39	7.03	+0.19
	Nov. 18 to 19	0.5	do	12	−3.00	0.00	−3.00	0.00	1.15	1.40	1.16	1.35	1.60	6.34	6.08	+0.06
	Dec. 17	0.5	do	11	−3.50	−0.20	−3.90	−0.80	1.00	1.60	1.02	1.03	1.63	5.94	6.48	+0.23
	1937															
	Feb. 10	0.5	do	12	−3.20	+0.20	−3.50	−0.40	1.60	1.50	0.91	1.46	1.36	6.04	6.38	0.00
	Mar. 9	0.5	do	12	−3.30	−0.10	------	−0.40	1.40	1.80	1.14	1.62	2.02	------	------	------
	Apr. 13	0.5	do	10	−3.20	−1.00	−3.30	−0.40	1.90	1.90	0.75	1.42	1.42	6.24	6.18	0.00
	1936															
2	Sept. 24	0.5	do	20	−4.00	−0.50	−4.00	−0.10	1.00	0.60	1.56	1.45	1.05	6.34	6.08	−0.14
	Oct. 28	0.5	do	16	−2.70	−0.20	−3.65	0.00	1.10	1.30	0.81	0.87	1.07	5.39	7.03	+0.16
	Nov. 18 to 19	0.5	do	18	−3.20	+0.25	−2.80	0.00	0.85	1.00	1.16	1.00	1.15	6.74	5.68	0.00
	Dec. 17	0.5	do	18	−3.50	−0.30	−3.80	−0.10	0.60	1.10	1.02	0.62	1.12	6.04	6.38	+0.17
	1937															
	Feb. 10	0.5	do	20	−3.40	−0.30	−4.20	0.00	1.00	1.10	0.91	0.91	1.01	5.54	6.88	+0.10
	Mar. 9	0.5	do	19	−3.20	−0.60	------	−0.20	1.10	1.20	1.14	1.26	1.36	------	------	------
	Apr. 13	0.5	do	16	−3.70	0.00	−3.50	−0.20	1.30	1.40	0.75	0.96	1.06	6.54	5.88	−0.01

TABLE 4.—*Current measurements in the York River in 1936 and 1937*—Continued

Station No.	Date	Length of series	Method of observation	Average depth	Current intervals: Slack before flood	Strength of flood	Slack before ebb	Strength of ebb	Observed velocity: Flood	Ebb	Correction factor	Corrected velocity: Flood	Ebb	Duration: Flood	Ebb	Resultant[1] or nontidal current
	1936															
		Days	Meter	*Feet*	*HW+*	*HW+*	*LW+*	*LW+*	*Knots*	*Knots*		*Knots*	*Knots*	*Hours*	*Hours*	*Knots*
3	Aug. 10 to 11	1.0	do	0.8 to 1.3	−4.00	−0.40	−4.40	−1.80	0.90	0.75	1.10	0.98	0.83	5.94	6.48	−0.02
	Sept. 25	0.5	do	1.7	−3.50	−1.20	−4.80		0.70					5.04	7.38	
	Oct. 29	0.5	do	1.5 to 2.0	−3.00	−0.50	−4.10		1.00	1.00	0.72	0.72	0.72	6.14	6.28	+0.01
	Nov. 19	0.5	do	1.4	−3.80		−4.50	−1.70	0.70	0.90	1.19	0.85	1.05	5.64	6.78	+0.11
	Dec. 18	0.5	do	1.6	−4.10	−0.90	−4.60	−1.60	0.80	0.80	1.04	0.83	0.83	5.84	6.58	+0.03
	1937															
	Feb. 9	0.5	do	1.8	−3.60	−0.50	−3.80	−1.10	0.80	0.80	1.02	0.82	0.82	6.14	6.28	+0.01
	Mar. 10	0.5	do	1.6	−4.00		−4.00	−1.90		1.20				6.34	6.08	
	Apr. 14	0.5	do	2.6	−2.80	−0.30	−3.90	−1.60	1.30	1.40	0.79	1.02	1.12	5.24	7.18	+0.17
	1936															
3	Aug. 10 to 11	1.0	do	3.0 to 5.3	−4.05	−1.00	−4.40	−1.80	0.70	0.70	1.10	0.77	0.77	5.99	6.43	+0.02
	Sept. 25	0.5	do	6.8	−3.20	−0.80	−4.70		0.70					4.84	7.58	
	Oct. 29	0.5	do	5.2 to 7.3	−4.10	−0.80	−4.00		0.90	0.80	0.72	0.66	0.56	6.44	5.98	−0.05
	Nov. 19	0.5	do	5.6	−3.40	−0.90	−4.50	−1.20	0.80	0.90	1.19	0.96	1.06	5.24	7.18	+0.12
	Dec. 18	0.5	do	6.4	−4.40	−1.10	−3.90	−1.00	0.60	0.90	1.04	0.63	0.93	6.84	5.58	+0.05
	1937															
	Feb. 9	0.5	do	7.2	−3.60	−0.50	−3.90	−0.90	0.70	0.70	1.02	0.71	0.71	6.04	6.38	+0.01
	Mar. 10	0.5	do	6.4	−3.60		−3.50	−0.90		0.70				6.44	5.98	
	Apr. 14	0.5	do	10.4	−3.30	+0.10	−3.80	−1.30	1.10	1.00	0.79	0.88	0.78	5.84	6.58	+0.01
	1936															
4	Sept. 23	0.5	do	6	−3.80	+0.10	−4.20	−2.10	1.10	0.80	1.51	1.58	1.28	5.94	6.48	−0.07
	Oct. 29	0.5	do	5	−3.30	−0.60	−4.0	−0.80	1.40	0.70	0.72	1.11	0.41	5.64	6.78	−0.16
	1936															
4	Sept. 23	0.5	do	16	−3.90	−0.10	−4.20	−1.50	1.20	0.80	1.51	1.71	1.31	6.04	6.38	−0.11
	Oct. 29	0.5	do	12	−3.30	−0.80	−3.80	−0.70	1.20	1.00	0.72	0.89	0.69	5.84	6.58	−0.02
	1936															
4	Sept. 23	0.5	do	25	−3.55	−0.30	−4.00	−0.80	0.90	0.80	1.51	1.33	1.23	5.89	6.53	0.00
	Oct. 29	0.5	do	20	−3.30	−0.90	−3.80	−0.60	1.00	0.70	0.72	0.76	0.46	5.84	6.58	−0.06
	1937															
4A	Apr. 29	0.5	Pole	2	−2.80	−0.40	−4.90	−1.90	0.60	0.90	1.16	0.72	1.02	4.24	8.18	+0.25
	Apr. 29	0.5	Meter	2	−2.40	−0.50	−4.60	−1.80	0.70	1.00	1.16	0.84	1.14	4.14	8.28	+0.28
	Apr. 29	0.5	do	5	−2.80		−4.60	−1.80		0.90				4.48	7.94	
	Apr. 29	0.5	do	8	−2.60	−0.50	−4.60	−2.20	0.60	0.80	1.16	0.71	0.91	4.34	8.08	+0.20
	Mean values as derived from the entire series															
1	Aug. 10, 1936, to Apr. 29, 1937.	4.0	Pole	7	−3.10	−0.21	−3.77	−0.22	1.66	1.78	0.98	1.63	1.75	5.67	6.75	+0.13
		19.0	Meter	7	−2.98	−0.01	−3.45	−0.11	1.54	1.56	1.02	1.57	1.59	5.87	6.55	+0.10
		19.0	do	18	−3.24	−0.22	−3.45	−0.16	1.62	1.42	1.02	1.65	1.45	6.13	6.29	−0.05
		19.0	do	29	−3.44	−0.35	−3.54	−0.27	1.33	1.10	1.02	1.35	1.12	6.24	6.18	−0.08
2	Sept. 24, 1936, to Apr. 13, 1937.	1.5	Pole	2	−2.70	−0.20	−3.87	−0.13	1.60	1.73	1.01	1.62	1.75	5.17	7.25	+0.22
		3.5	Meter	5	−3.07	−0.28	−3.71	−0.16	1.36	1.93	0.99	1.34	1.91	5.70	6.72	+0.27
		3.5	do	11	−3.19	−0.26	−3.56	−0.26	1.35	1.53	0.99	1.34	1.52	5.97	6.45	+0.09
		3.5	do	18	−3.39	−0.18	−3.66	−0.09	0.98	1.10	0.99	0.97	1.09	6.07	6.35	+0.05
3	Aug. 10, 1936, to Apr. 14, 1937.	2.0	Pole	2	−3.40	−0.87	−4.25	−1.50	0.85	0.80	0.93	0.79	0.74	5.49	6.93	+0.05
		4.5	Meter	2	−3.74	−0.63	−4.28	−1.64	0.89	0.95	1.00	0.89	0.95	5.80	6.62	+0.06
		4.5	do	7	−3.74	−0.71	−4.10	−1.27	0.78	0.80	1.00	0.78	0.80	5.98	6.44	+0.03
4	Sept. 23 to Oct. 29, 1936.	1.0	Meter	6	−3.63	−0.25	−4.10	−1.45	1.25	0.75	0.98	1.23	0.73	5.87	6.55	−0.12
		1.0	do	14	−3.70	−0.45	−4.00	−1.10	1.20	0.90	0.98	1.18	0.88	6.04	6.38	−0.08
		1.0	do	22	−3.47	−0.60	−3.90	−0.70	0.95	0.75	0.98	0.93	0.73	5.91	6.51	−0.04

[1] A plus (+) sign denotes downstream and a minus (−) sign denotes upstream resultant or nontidal current.

of this recent survey, the cross-sectional area was found by the authors to be equal to 77,308 square feet at mean low water, and 92,718 square feet at mean high water. These figures give satisfactory agreement with the computations based on the 1911 survey.

From the current-meter observations at four stations across the river, the stream flow for flood and ebb tide was estimated by computing the average velocity of current, which is equal to the velocity at the strength of the tide multiplied by 0.637, and by the duration of flood or ebb tide. The resulting nontidal current, or the excess of ebb over flood tide, was then calculated for each section. In sections A and L the velocities and durations were estimated. By summing all the areas, the following final figures

were obtained. Total flow of the river at Purtan Bay during flood period amounted to 2,235,416,000 cubic feet; during ebb period, 2,484,875,000 cubic feet; ebb excess, 249,459,000 cubic feet. By dividing the excess ebb flow by the area of the cross section multiplied by tidal cycle (12.42 hours, or 44,712 seconds) we obtained the value of the nontidal current, which was found to be equal to 0.0686 foot per second, or 0.04 knot, downstream.

As to the distance traveled by a particle during a tidal cycle, this can be computed for any station by making use of the fact that a current curve approximates a cosine curve, and on a cosine curve it is known that the ratio of the mean ordinate to the maximum ordinate is $2 \div \pi$, or 0.6366. Since the strength of the tidal current corresponds to the maximum ordinate, it follows that during any given flood or ebb period the average current will be the strength of the current multiplied by 0.6366. The horizontal distance traveled by a particle or floating object, therefore, would be given by multiplying the average velocity during any flood or ebb period by the corresponding duration of flow.

It should be noted that this formula can give only approximate results, for the use of the cosine relationship gives only an approximate value of the average current. Furthermore, even more serious is the assumption made in the formula that the floating object during the various stages of its journey will experience the same changes in velocity which occur at the point where it started.

In order to determine the direction that effluents leaving the pulp mill at West Point would take on an ebb tide and the distance that a particle would travel downstream, a study was made using floats released off the pulp mill at high-water slack on October 17, 1938.

Each float consisted of two citrate bottles fastened one above the other by cord so that the total height was 24 inches. Sand in the bottles was adjusted so that they would float with less than a half inch of the top of the upper bottle exposed to the air. Visibility of the floats was increased by the use of small flags made from bicycle spokes to which were fastened small pieces of white cloth. The floats were followed by boat, and observations of the position of the floats were made at half-hour intervals during a complete change of tide on October 17, 1938, starting at high-water slack at 6:30 a. m. off the pulp mill at West Point. Observations were continued to high-water slack late that afternoon. Neap tides occurred during this period, the moon being in the last quarter. The predicted times of tides and currents are given in table 5. The weather was clear with almost no wind all day so that the water was perfectly smooth. A dense fog settled down for a period of about an hour and a half in the late forenoon so that visibility was poor during that time. The course of the bottles during the ebb and flood tides is shown on the map presented in figure 7.

TABLE 5.—*The predicted times of tides and currents of the upper York River on Oct. 17, 1938* [1]

TIDE AT WEST POINT

Latitude 37°32′, Longitude 76°48′

Tide	*Time*	*Height, in feet*
High water	5:18 a.m.	2.9
Low water	11:35 a.m.	0.8
High water	5:49 p.m.	3.2

CURRENT AT WEST POINT

Tide	*Time*	*Velocity, in knots*
High-water slack	6:16 a.m.	----------
Greatest ebb	10:42 a.m.	2.1
Low-water slack	2:11 p.m.	----------
Greatest flood	4:58 p.m.	1.5

CURRENT ¾ MILE BELOW WEST POINT

Latitude 37°31′, Longitude 76°48′

Tide	*Time*	*Velocity, in knots*
High-water slack	5:21 a.m.	----------
Greatest ebb	9:47 a.m.	1.5
Low-water slack	1:16 p.m.	----------
Greatest flood	4:03 p.m.	1.1

[1] Data were obtained from the Tide Tables, Atlantic Ocean, and Current Tables, Atlantic Ocean, North America, published by the U. S. Coast and Geodetic Survey.

At high-water slack 10 floats were released off the unloading platform at the mill. Three were lost immediately, probably as a result of sinking caused by improper adjustment of the sand. Visibility in this area was poor at this time, because of the steaming of the water. The river near the mill was brown with mill effluent and felt hot. A surface thermometer showed that the water of this area had a temperature of 76° F., while that of the river elsewhere had a temperature of 64° F. The water was discolored brown with the effluent for a distance of about 1½ miles, as far down as West Point Bar. The remaining bottles separated; four went slightly offshore and upstream with the last of the flood tide that was still running in the channel, and three went downstream with the first of the ebb tide running along the shore, where they became entangled with barges tied along the shore and had to be taken out and started again in the channel. From the place

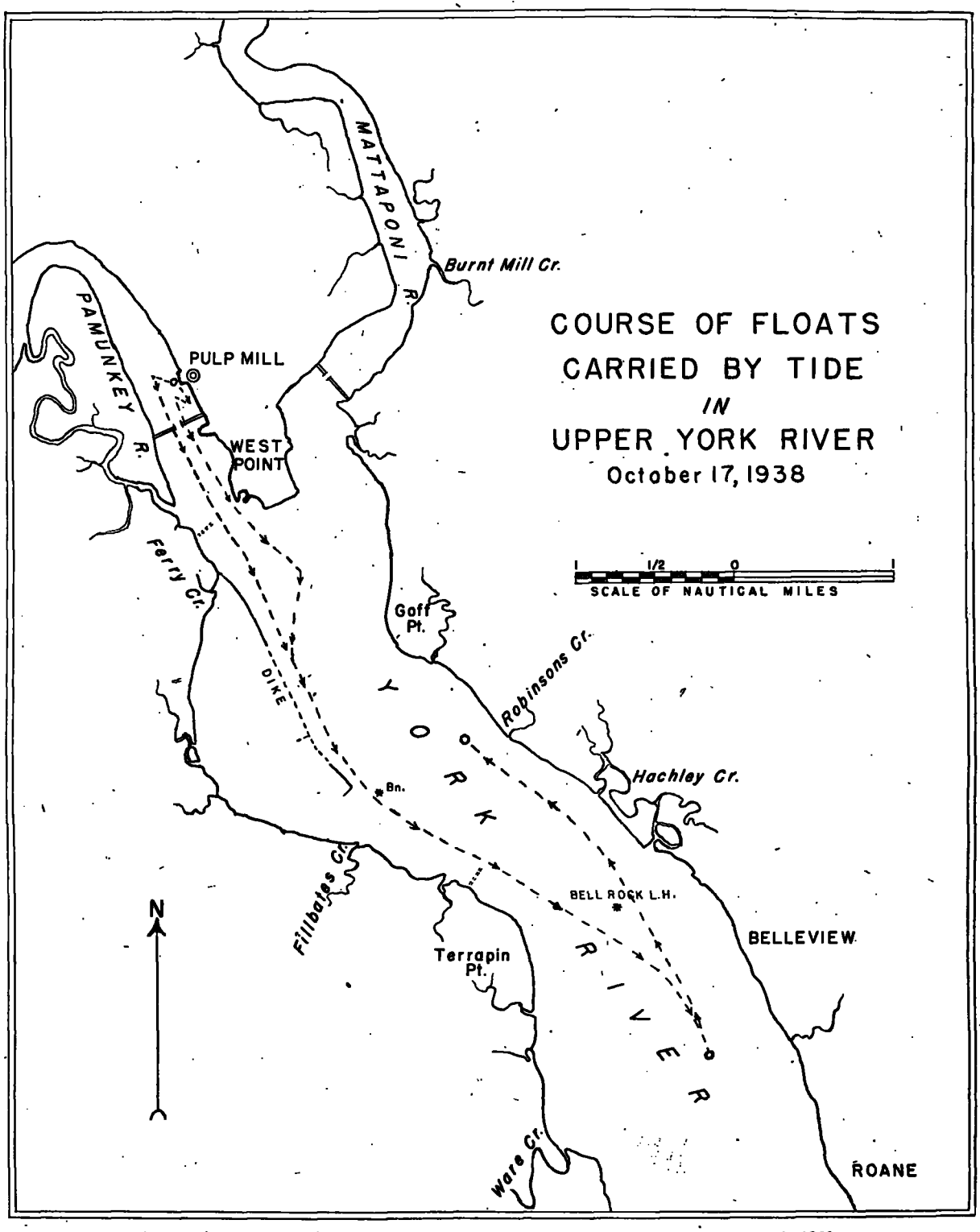

FIGURE 7.—Course of floats carried by the tide in the upper York River on October 17, 1938.

of release they floated along the shore past West Point and curved in across West Point Bar nearly to the channel of the Mattaponi River, then, turning back, joined the others coming down the right edge of the channel of the Pamunkey River. From this point all the bottles kept well together and passed down the river just inshore of the black buoys on the right edge of the channel to the bell buoy at Bell Rock. Here they went across the channel and continued down the left edge of the channel to a point about half way between Bell Rock Light and Roanes Point Beacon. The lowest point reached on this tide was about 5¼ miles from the place of release.

On the following flood tide the floats moved slowly up the river; they crossed the channel toward the left shore of the river, going in the water from 6 to 10 feet deep, and passed well inshore of Bell Rock Light. When the tide slacked off and further observations were discontinued, they had reached the point just above Robinson's Creek.

It is of interest to note that on October 19 one of the floats was recovered 5 miles above West Point in the Pamunkey River. This float must have become entangled with the barges at the start and then traveled upstream on a flood tide.

TEMPERATURE

Temperature observations of the bottom water of the York River at Naval Mine Depot just above Yorktown were made continuously by means of a gas-operated recording thermometer. The sensitive bulb was held just off the bottom, placed with its cable inside a capped galvanized pipe. Slots along the sides of the pipe in the vicinity of the bulb allowed a ready interchange of the water. The depth of water at the location of the instrument was 12 feet at mean low water. Observations were started on October 19, 1935. The water temperature for each hour from midnight of one day to midnight of the next was taken from the chart, and the minimum, maximum, and mean for the day noted.

Observations of surface-water temperatures of the Pamunkey River at Bruce Memorial Bridge at West Point were made by use of an ordinary mercury thermometer at high and low water each day starting May 1, 1936. With the deep-sea reversing thermometer, readings were made at high and low water off the steamboat dock at Yorktown three times a week at both surface and bottom. Water temperatures at the various hydrographical stations in the York and Piankatank Rivers were ascertained at various times. Observations of water temperatures were also made in studies of isohalines and tidal cycles at various places and times throughout the investigation.

The climatological conditions of the area of the York and Piankatank Rivers were unusual in many respects during the time of the investigations. Unusually cold weather with considerable snow characterized the first winter. December 1935 was next to the coldest December on record, while January and February 1936 were the fourth and eighth coldest on record. Unusual ice conditions prevailed with considerable portions of the York and Piankatank Rivers frozen. March 1936 was unusually warm, and air temperatures from May to October of that year averaged above normal with many record-breaking maxima observed during June and July. The winter of 1936–37 was mild, and air temperatures during January 1937 were unusually high, being the next highest on record.

Minimum and maximum air temperatures were taken from the records of the nearest meteorological station at Williamsburg, Va., as reported in the Climatological Data, United States Department of Agriculture, Virginia section. These were averaged for 5-day periods and are shown in figure 8. The maximum temperature during the period from October 1935 to July 1937 occurred on June 30, 1936, with an air temperature of 102° F. (38.9° C.), and the minimum occurred on February 1, 1936 with a temperature of 0° F. (−17.8° C.).

Considering the records obtained at the Naval Mine Depot station, shown in figure 8, the water temperature fluctuated but slightly from day to day. There was a general rise in the spring and summer and a drop in late summer and fall. Starting October 19, 1935, the records show a drop from temperatures of about 20° C. Unusually cold weather in December 1935 and again the last of January 1936 resulted in exceptionally low-water temperatures. The lowest temperature occurred on February 7 and 8, 1936, when readings of −1.5° C. were observed. At this time much of the river was covered with ice, even as far down as Yorktown. The water temperature rose rather rapidly and continued to rise until July and August. The maximum of the summer occurred on August 25 and 26, 1936, when a temperature of 29.5° C. was recorded. The drop in water temperature following the maximum was rather regular until January 1937, when there was a very marked rise which reflected the unusually

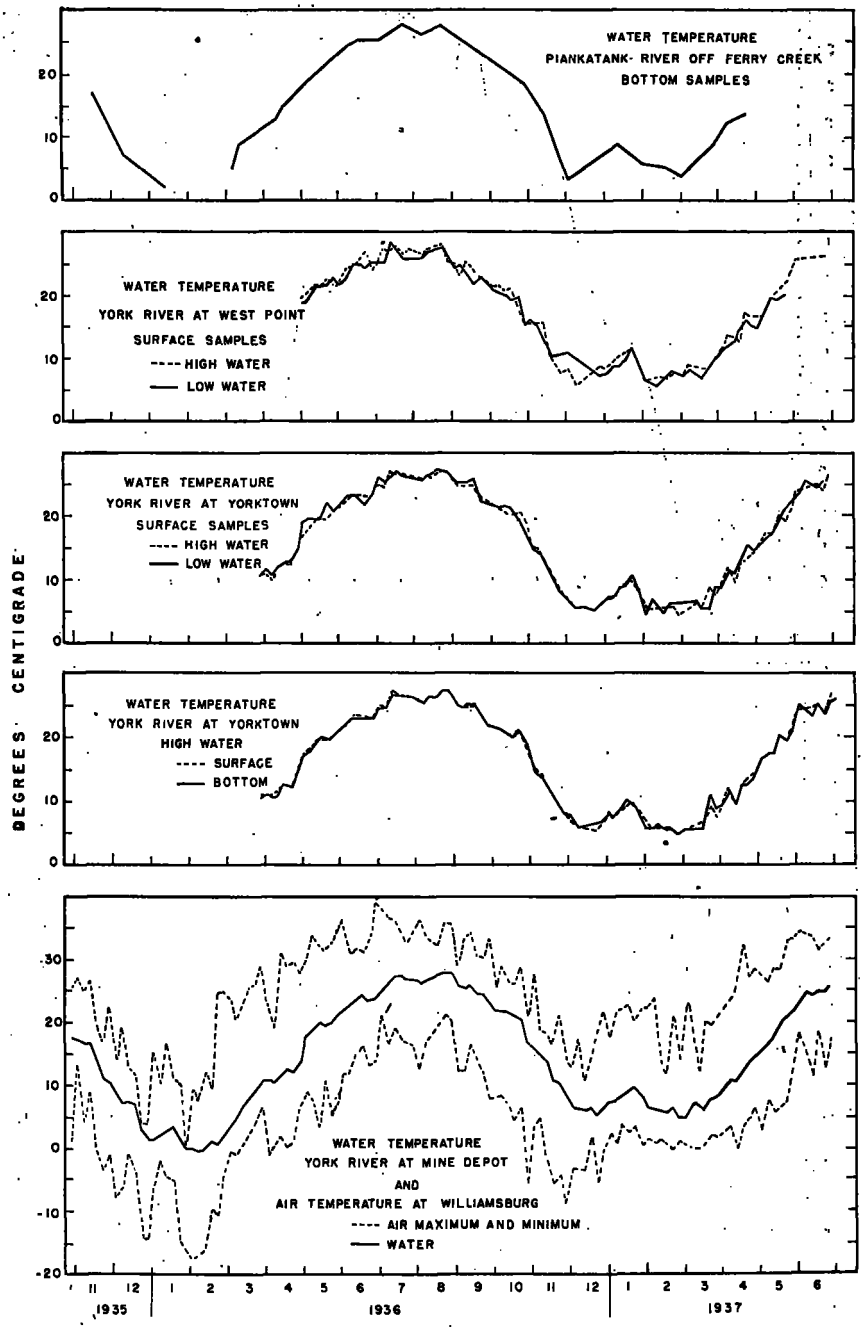

FIGURE 8.—Seasonal changes in air and water temperature in the York and Piankatank Rivers. The plotted points represent 5-day averages.

high air temperatures. The minimum for the winter of 1936–37 occurred on March 1, when 3.5° C. was recorded. A gradual increase in the water temperature followed during the spring.

It will be noted from the comparison of water and air temperatures in figure 8, that the water warmed more slowly than the air during the spring and cooled more slowly during the fall.

Similar seasonal changes in water temperature were observed at West Point, although the records were not so complete. The observed water temperatures at high water and low water, grouped in 5-day

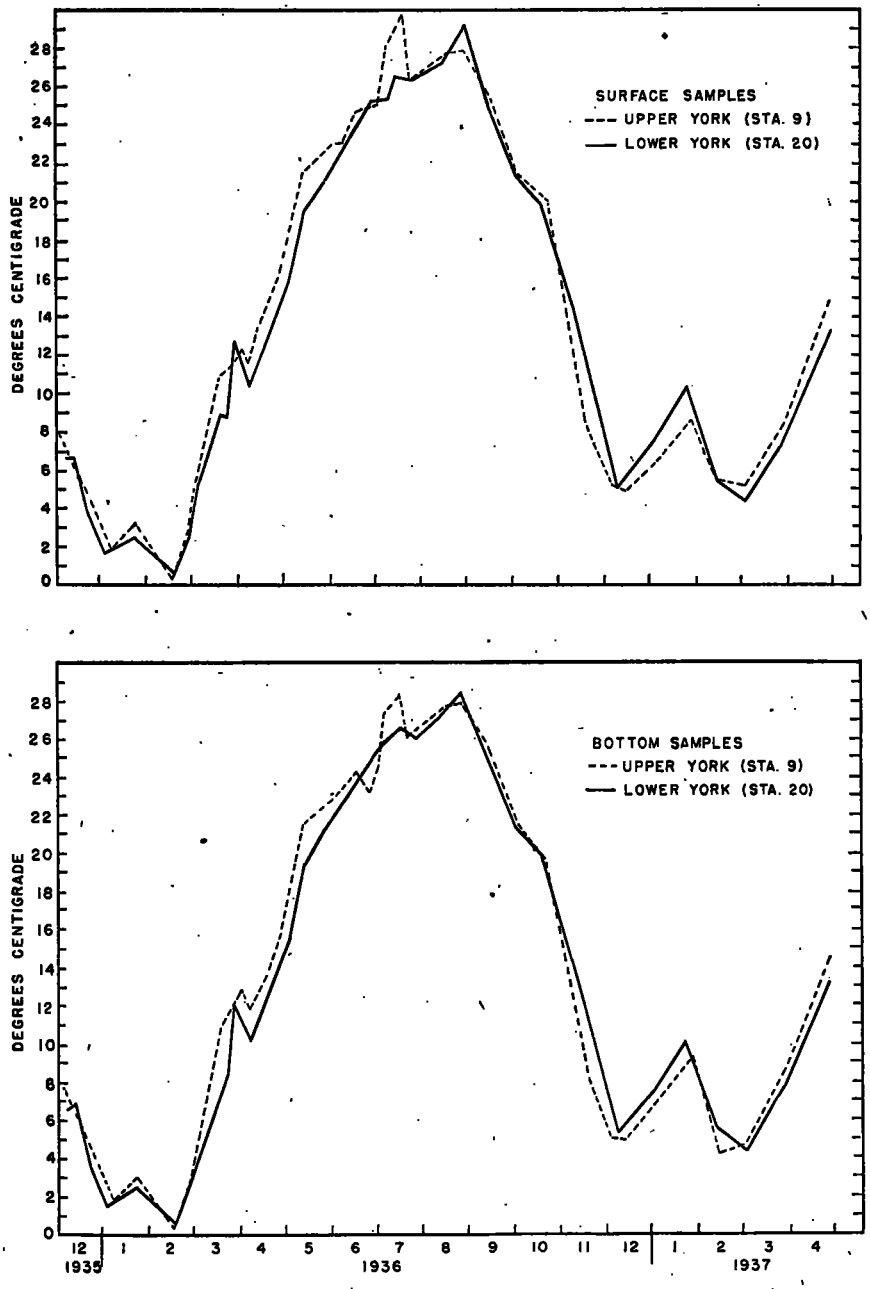

Figure 9.—Water temperatures in the lower (station 20) and upper (station 9) parts of York River.

periods, are shown in figure 8. Starting May 1, 1936, with temperatures of 18° C. at low water and 20° C. at high water, there was a gradual warming of the water during the spring and early summer. The maximum temperature of 29° C. was recorded July 14 and 18, 1936, and again on August 22, 1936. Following this, the water cooled during the fall. A marked rise occurred during the warm weather of January 1937. The minimum was 5° C. on February 11 and 12. The following spring the water warmed gradually and reached 29° C. on June 21, 1937.

The water temperature at Yorktown followed the same seasonal changes. Observations made three times a week at high water and low water at the surface and bottom are shown in the curves in figure 8. During the period from March 26, 1936, to July 1, 1937, the minimum water temperature

was 4.1° C. on March 1, 1937, and the maximum 29.6° C. on August 25, 1936.

Similar seasonal changes were observed in the Piankatank River (fig. 8) and at other stations at which temperature of the water was measured (tables 6–20, pp. 177–186).

As for the horizontal distribution of water temperatures in the York River, it was observed that there was but slight variation throughout its length. The upper portion of the river had a slightly warmer temperature during the spring and summer than the lower, but during the winter this situation was reversed. The changes, however, were remarkably slight. The amount of fresh water entering the York River from above appears to have but slight influence in warming the water in the summer and cooling it in the winter. Figure 9 shows a comparison of the water temperatures at station 20 in the lower York and station 9 in the upper York Rivers. It will be noted that, although the differences in water temperature were very slight, the upper river warmed earlier in the spring and was warmer than the lower during the summer. There was little difference during the late summer and fall. In the winter the lower river was slightly warmer than the upper. This was due to the influence of the warmer sea water of Chesapeake Bay at that time of year.

Differences in the vertical distribution of water temperature were nearly absent except at the deeper stations. It will be seen that the curves showing water temperatures at high water at the surface and bottom (14 ft.) at Yorktown are almost identical (fig. 9). The surface water warmed more quickly than the bottom water during the spring.

Tidal effects on water temperature were unimportant. A comparison of water temperatures at Yorktown and West Point at high water and at low water throughout the season (fig. 8) shows almost no differences at those stages of tide. Observations made of changes throughout tidal cycles show that the effect of time of day on water temperature was more important than the stage of tide.

TURBIDITY

Data on the relative turbidity of the water at the various stations in the York and Piankatank Rivers were obtained throughout the time of observations. Measurement was made through the use of a Secchi disk, 6 inches in diameter, which was lowered and then raised, the depth at which it disappeared on lowering and reappeared on raising being determined by several trials and recorded to the closest tenth of a meter. The observations for two stations, station 9 of the upper York and station 20 of the lower York, are compared in figure 10. The results of measurements at all stations are given in tables 6 to 20 (pp. 177–186).

Precipitation conditions have an important bearing on the turbidity of the water. Precipitation records from the Climatological Data, United States Weather Bureau, for the period from October 1935 through June 1937 at stations on the York watershed are presented in the graph in figure 10.

During September 1935 there was considerable rainfall in the area of the York watershed, and many of the streams were at flood stage. January, March, and December 1936 were unusually wet months, January exceeding all former records. Dry weather characterized the period from May to August 1936, the amount for May being the next to the least on record. The year 1937 was the wettest year on record, and in January 1937 there occurred the greatest precipitation ever recorded for that month. April and August were the third wettest, while March was unusually dry. Noteworthy floods occurred throughout the streams of the area during April 1937.

There was an increased turbidity throughout the spring of the year 1936. This was followed by a decreasing turbidity through the summer and fall, the summer of this year being particularly dry as well as being the time of year of least run-off. Increased rainfall during January 1937 brought about an increased turbidity, which was continued throughout the following spring. Unusually high rainfall in April 1937 caused a marked increase in turbidity, the water appearing brownish red even below Yorktown.

The water of the upper part of the York River was consistently more turbid than that of the lower section where fluctuations in turbidity were more pronounced. Disk readings at station 9 of the upper river ranged from 0.2 meter to 1.0 meter, and averaged 0.47 meter. In the lower York at station 20 the range was from 0.7 meter to 2.0 meters, and the mean was 1.39 meters.

The Piankatank River was clear throughout the time of the investigations. The disk could be seen clearly on the bottom in the lower river at each sampling. The upper part of the river was more turbid than the lower but still much less turbid than the York River. The readings at station 53 in the

upper Piankatank ranged from 0.5 meter to 2.2 meters, or bottom, the mean being 1.44 meters.

SALINITY

The salinity in a tidal river is in a state of unstable equilibrium which, for each given point, is determined by its distance from the mouth, the stage of the tide, and the river discharge. Under these conditions daily and seasonal fluctuations are to be expected. Furthermore, from the head of the river toward its mouth, there must be a definite salinity gradient, which also changes with the river stage. Observations made in the York and the Piankatank Rivers show these conditions.

Samples for salinity were taken by means of the Eckman bottle and transferred to citrate bottles with patent stoppers for transportation to the laboratory. In a few instances the salinity was computed from specific gravity determinations made by the use of standardized hydrometers, but in most cases the samples were titrated for chloride by the Knudsen method as described by Oxner (1920), and the salinity computed by the use of hydrographic tables (Knudsen 1901).

Observations of seasonal changes in salinity were made at the surface and the bottom for both high and low water three times a week from the steamboat dock at Yorktown, and for the surface at each tide at the Bruce Memorial Bridge at West Point. Salinity of the water was also determined at the various hydrographic stations of the York and Piankatank Rivers at regular intervals. Other observations included studies of the horizontal distribution of salinity at one tidal stage in the York and Piankatank Rivers, and studies of the changes in salinity of the water throughout tidal cycles at various localities. Seasonal changes in salinity at Yorktown and West Point are shown in figure 10. Observations at all the stations are reported in tables 6–20 (pp. 177–186).

At Yorktown during the period from March 1936 to July 1937 the salinity ranged from a minimum of 5.46 parts per thousand on May 5, 1937, to a maximum of 23.96 parts per thousand on October 15, 1936. When the observations were started in March 1936 the salinity was about 11 parts per thousand. There was a steady increase in salinity throughout the spring and summer. The salinity remained at a relatively high figure during the fall and early winter, dropping markedly in January 1937 as a result of considerable precipitation. During the following spring the salinity change was slight until the flood conditions of April 1937, when there was a sharp drop. This was followed by a rapid rise during May and June 1937.

Changes in salinity at West Point were much more abrupt. The range was from 0.08 part per thousand on January 22, 1937, and May 2, 1937, to 18.10 parts per thousand on October 27, 1936.

Observations made at station 53 off Ferry Creek in the Piankatank River from November 1935 to May 1937 show a minimum of 5.54 parts per thousand on May 6, 1936, and a maximum of 17.90 parts per thousand on November 10, 1936.

In general, it may be said that the seasonal changes in salinity followed the seasonal conditions of run-off, being high at the time of least run-off in the summer and fall and low during the time of greatest run-off in the spring, flood conditions being reflected by marked drops in salinity. The summer of 1936 being unusually dry, as well as being the season of least run-off, the salinity of the water was rather high. The relationship between salinity and precipitation can be seen by comparison of the curves in figure 10. The flood conditions of January and April 1937 are particularly marked in the resulting low salinity of the river at those times.

It is noteworthy that the range of salinity at Yorktown was 18.50 parts per thousand and at West Point was 18.02 parts per thousand.

Differences between surface and bottom salinities were very slight except at times of extreme floods (fig. 10). In general, the surface salinity was slightly less than the bottom salinity because of the flowing of the fresher water on top of the sea water.

The horizontal distribution of salinity of the York and Piankatank Rivers was studied at various times, samples being taken as nearly as possible at the same stage of tide throughout the river length. The results are presented in figures 11 and 12.

There was a gradual decrease in salinity from the mouth toward the head, depending on the amount of fresh water brought down the river from above and the inflow of salt water from Chesapeake Bay.

In the York River on March 17, 1936, at the last of ebb tide, the range of salinity was from 14.60 parts per thousand above Yorktown to 1.44 parts per thousand off Fillbates Creek. On December 15, 1936, the range at the last of flood tides was from 21.92 parts per thousand off Sandbox, below Yorktown, to 14.20 parts per thousand at a station in the Pamunkey River 1¾ miles above the bridge at West Point. On January 16, 1937, the range of

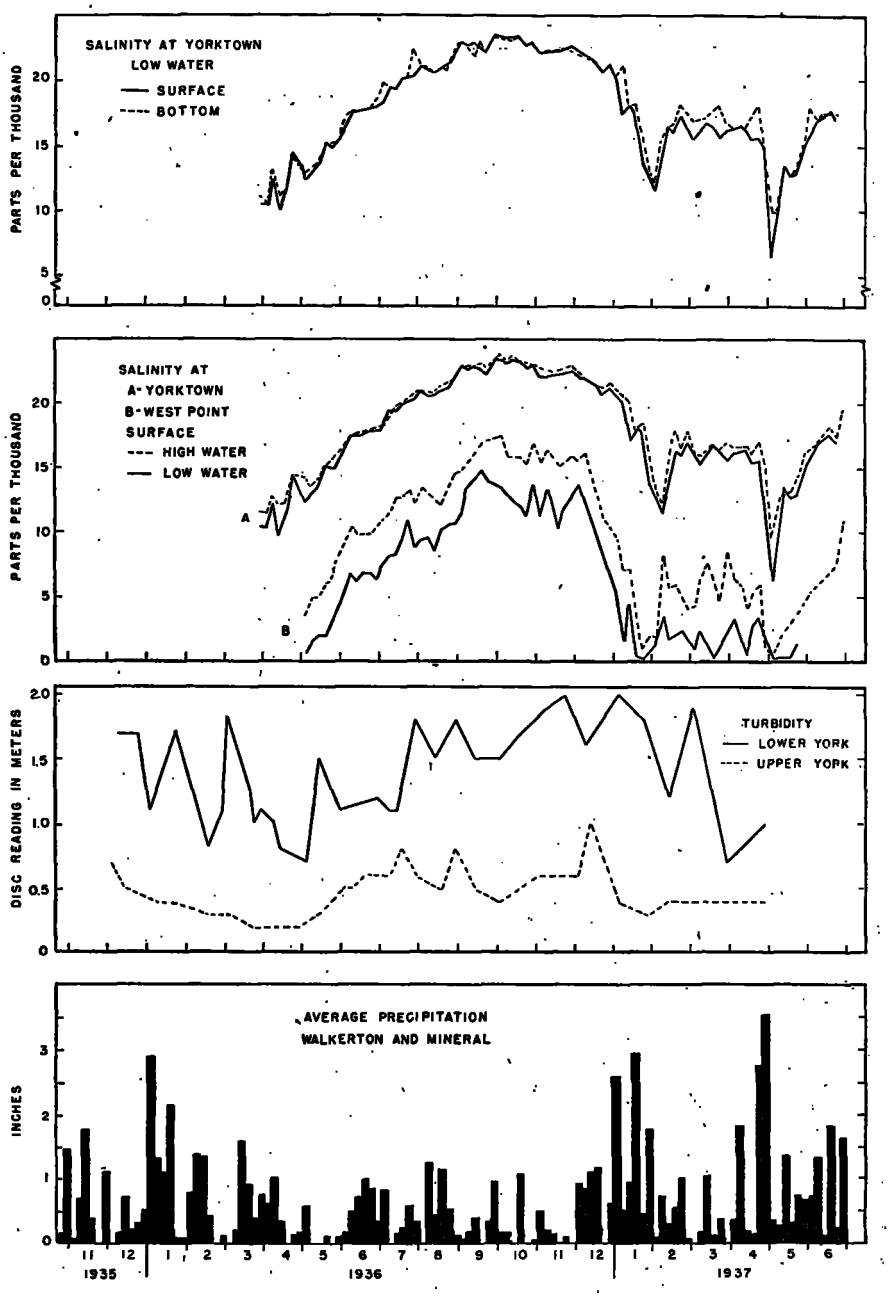

FIGURE 10.—Seasonal changes in precipitation in the York River drainage basin, the relative turbidity, and the salinity of the water of the upper and lower parts of the York River, from October 1935 to June 1937.

salinity at half-flood tide was from 19.45 parts per thousand off Carmines Islands to 2.65 parts per thousand at the above station in the Pamunkey River. On April 27, 1937, at the last of flood tide, the range was from 20.05 parts per thousand off Ellen Island to 14.83 parts per thousand at the above station in the Pamunkey River. On May 17, 1937, the range at the last of ebb tide was from 13.01 parts per thousand above Yorktown to 0.12 part per thousand at the above station in the Pamunkey River. At the last of flood tide on May 24, 1937, the range was from 15.25 parts per thousand above Yorktown to 1.89 parts per thousand at the above station in the Pamunkey River.

In the Piankatank River at the last of flood tide on May 5, 1936, the range in salinity was from 9.43

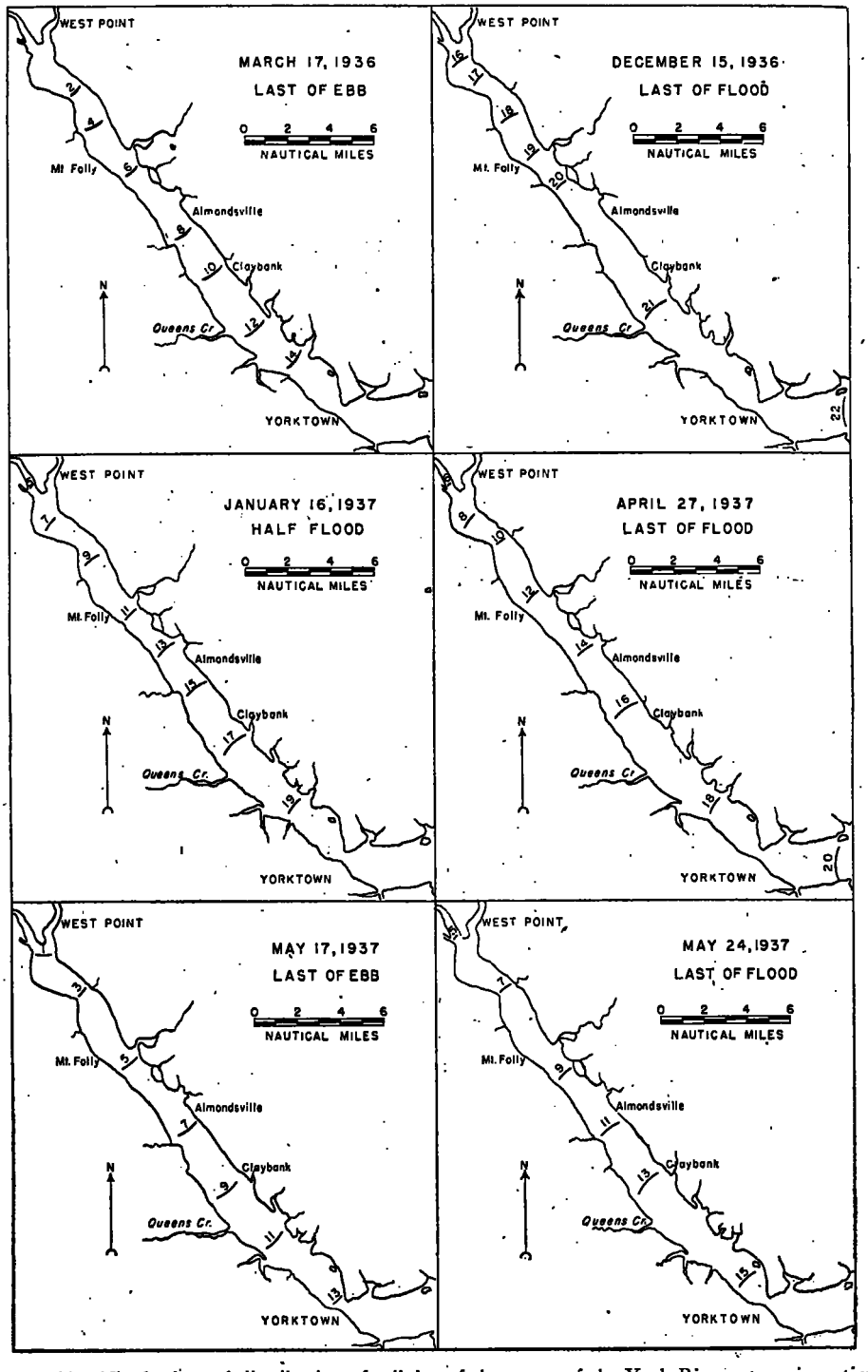

FIGURE 11.—The horizontal distribution of salinity of the water of the York River at various times. The numbers and heavy lines on the maps indicate isohalines in terms of salinity in parts per thousand.

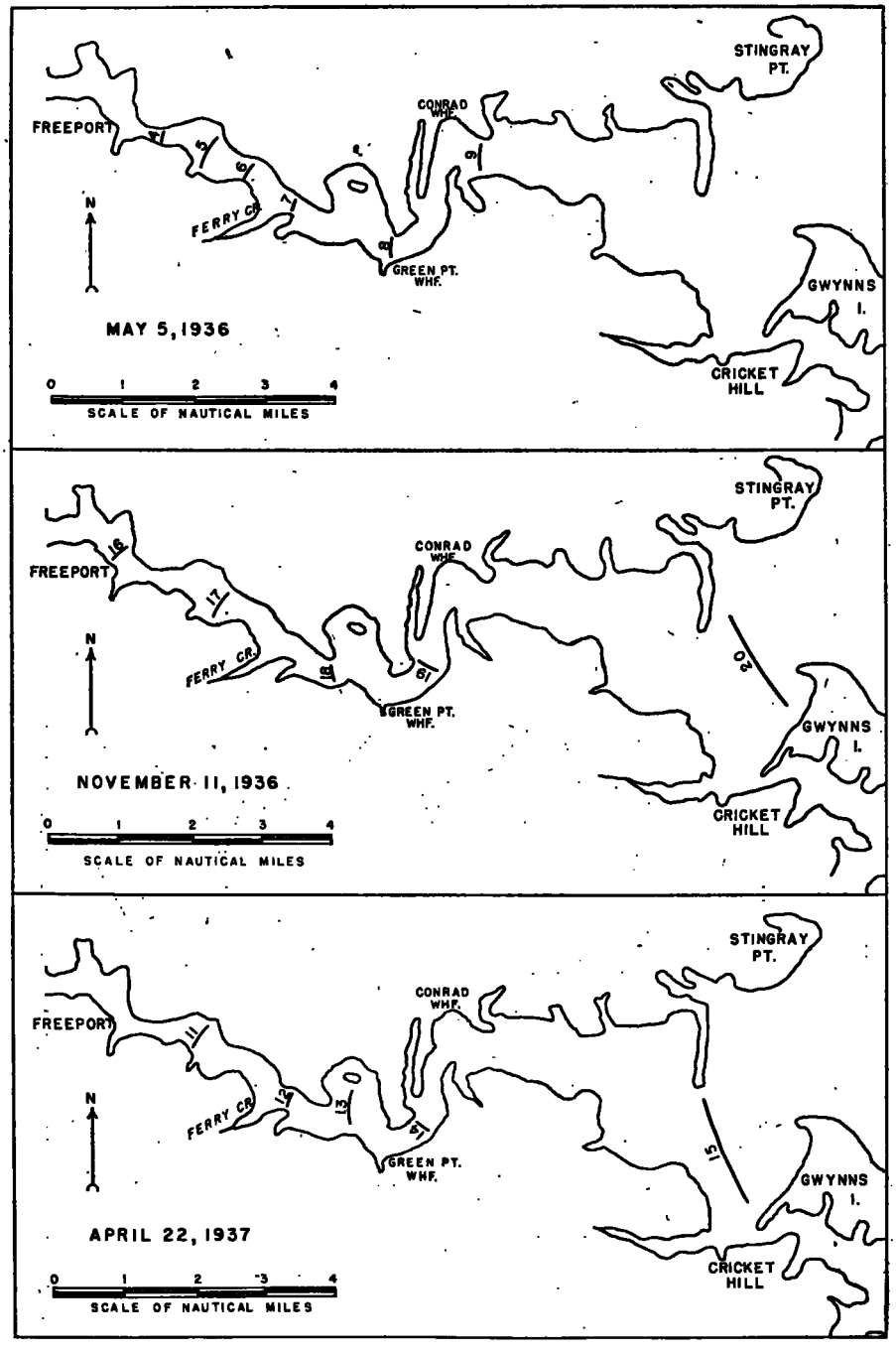

FIGURE 12.—The horizontal distribution of salinity of the water of the Piankatank River at various times. Observations were made during the last of flood tide on the dates indicated. The numbers and heavy lines on the maps indicate isohalines in terms of salinity in parts per thousand.

parts per thousand at the mouth to 3.60 parts per thousand at Freeport. On November 11, 1936, at the last of flood tide, the salinity ranged from 20.08 parts per thousand at the mouth to 15.99 parts per thousand at Freeport. On April 22, 1937, at the last of flood tide the range was from 15.18 parts per thousand at the mouth to 10.90 parts per thousand at a station off Bland Wharf, below Freeport.

The influence of tide on salinity was observed at various times at stations at Yorktown, Purtan Island, Bell Rock Lighthouse, and West Point. The results of these studies are shown in figures 13 to 20.

Figure 13 represents the tidal changes in salinity and temperature at Yorktown on February 24 and 25, 1936. It will be noted that at the bottom the highest salinity occurred 1¾ hours after high water and the lowest salinity occurred approximately one-half hour after low water. At the surface the highest salinity occurred 1¾ hours after high water and the lowest 1½ hours after low water. The salinity changes during this time were relatively small, varying from 12.99 parts per thousand to 16.24 parts per thousand at the surface, and from 14.78 to 19.11 parts per thousand at the bottom. The difference in salinity between high and low water was about 4 parts per thousand at the bottom and about 3 parts per thousand at the surface.

At a station just below West Point (fig. 14) on February 25 and 26, 1936, more marked differences between high and low water occurred. The salinity ranged from 0.59 part per thousand at low water to 6.53 parts per thousand at high water at the bottom, and from 0.11 to 6.31 parts per thousand at the surface. The surface salinity dropped more markedly after high water than did the bottom salinity, and the change of tide took place at the surface first at the start of ebb tide, and at the bottom first at the start of flood tide. The highest salinity at the sur-

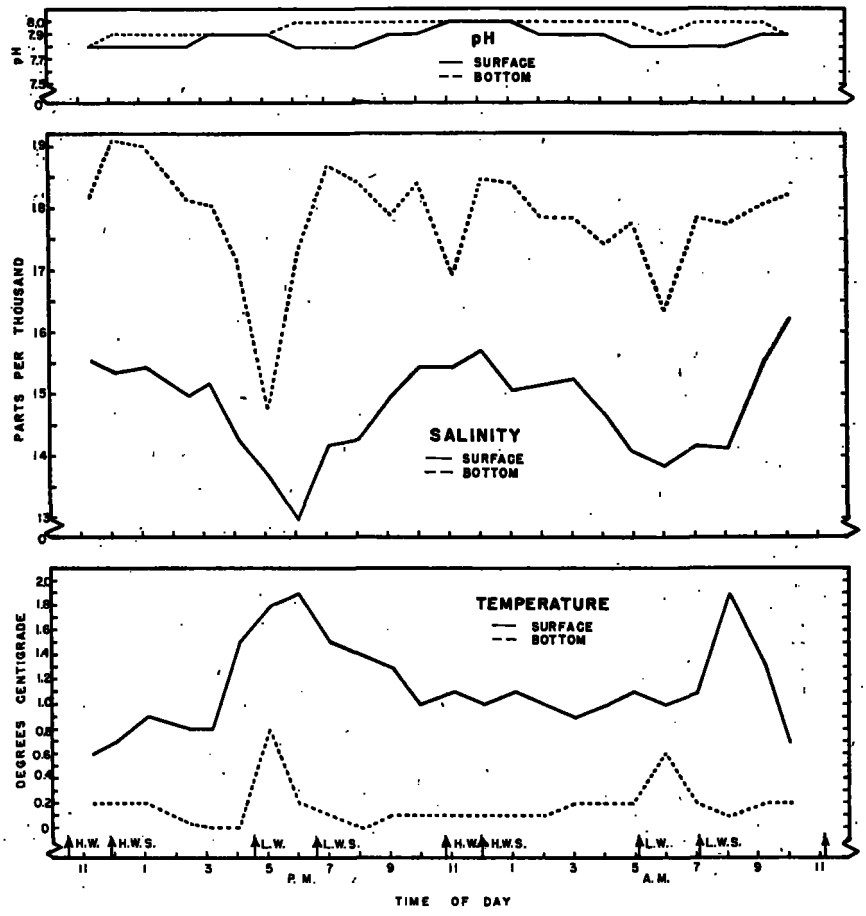

FIGURE 13.—Tidal changes in the temperature, salinity, and hydrogen-ion concentration of the water of the York River at Yorktown on February 24, and 25, 1936. Arrows indicate the stage of tide. L. W.=low water; L. W. S.=low water slack; H. W.=high water; H. W. S.=high water slack.

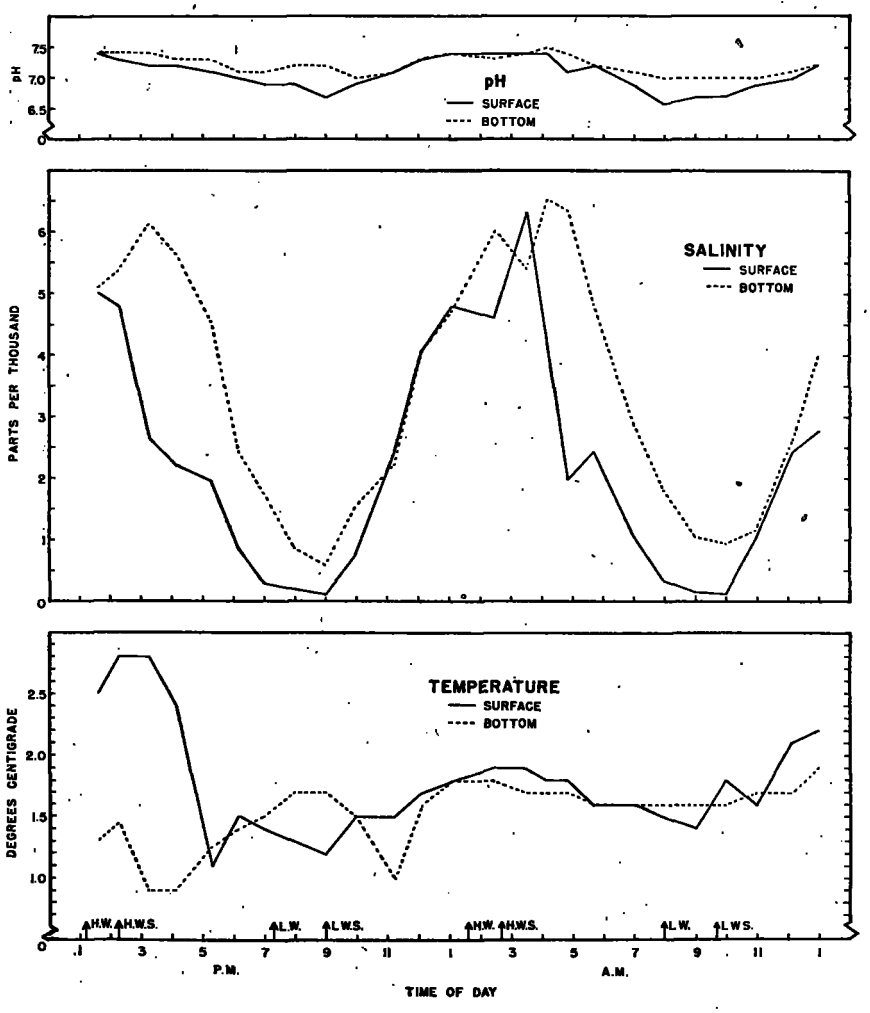

FIGURE 14.—Tidal changes in temperature, salinity, and hydrogen-ion concentration of the water of the York River just below West Point on February 25 and 26, 1936. Arrows indicate stage of tide. L. W.—low water; L. W. S.—low water slack; H. W.—high water; H. W. S.—high water slack.

face occurred approximately 2 hours after high water and at the bottom 2½ hours after high water. The lowest salinity occurred about 2 hours after low water.

Salinity changes during a tidal cycle at Yorktown on May 20, 1936, are shown in figure 15. Very slight differences were observed in salinity at high and low water, the range of salinity at the surface being only from 13.63 to 15.61 parts per thousand, and at the bottom from 14.36 to 16.04 parts per thousand. The highest salinity occurred one-half hour after high water and the lowest occurred 2 hours after low water.

Figure 16 shows the tidal changes in the Pamunkey River at West Point on May 21, 1936. The range of salinity was from 3.55 parts per thousand to 7.94 parts per thousand at the surface, and from 3.86 to 8.26 parts per thousand at the bottom. There was very little difference between surface and bottom samples. The highest salinity occurred about 2½ hours after high water and the lowest approximately 1½ hours after low water.

Salinity changes at Yorktown during a tidal cycle on September 24, 1936 (fig. 17) show a range from 18.75 parts per thousand to 20.26 parts per thousand for the surface water and from 19.47 parts per thousand to 20.95 parts per thousand for the bottom water. The highest salinity occurred about 2½ hours after high water at the surface and 2¾ hours after high water at the bottom. The lowest salinity was observed 2½ hours after low water.

During the tidal cycle studied at Yorktown on

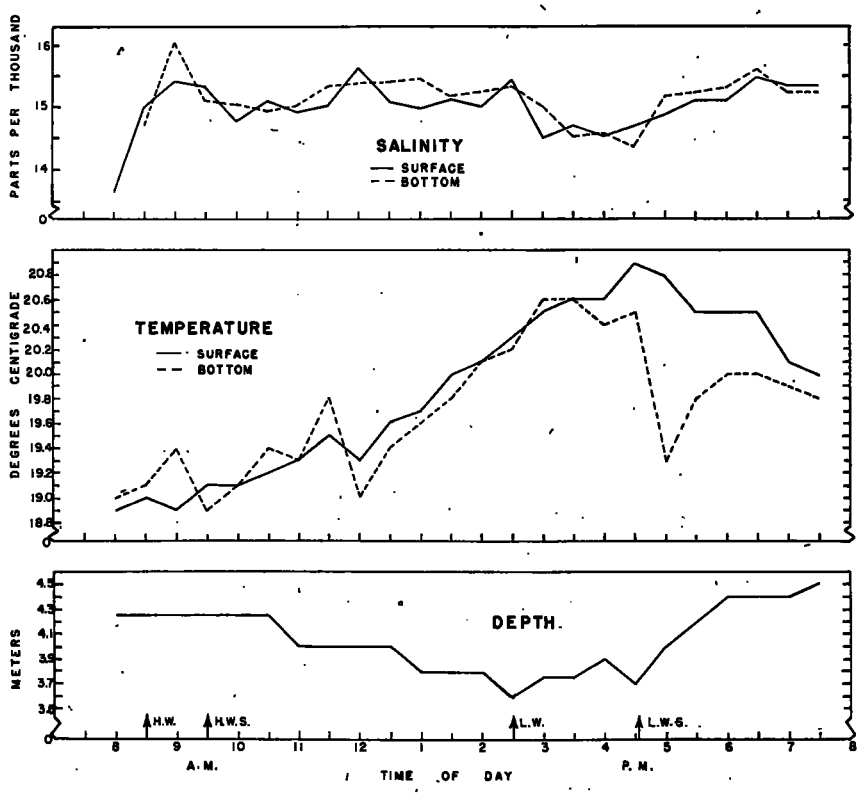

FIGURE 15.—Tidal changes in temperature and salinity of the water of the York River at Yorktown on May 20, 1936. Arrows indicate stage of tide. L. W.—low water; L. W. S.—low water slack; H. W.—high water; H. W. S.—high water slack.

October 29, 1936 (fig. 17), it was observed that the salinity range of the water at the surface was from 19.00 to 20.91 parts per thousand. At the bottom the range was from 19.63 to 21.24 parts per thousand. The highest salinity at the surface occurred 1¼ hours after high water and at the bottom 2¼ hours after high water. At the surface the lowest salinity was found 3¾ hours after low water and at the bottom 2¾ hours after low water.

Figure 18 shows the results of observations of salinity of the surface water during a tidal cycle off Purtan Island on February 10, and April 13, 1937. The salinity on February 10 ranged from 11.62 parts per thousand to 13.62 parts per thousand. The highest salinity was observed 1½ hours after high water, and the lowest salinity occurred approximately 2 hours after low water.

On April 13, 1937, the salinity of the bottom water during a tidal cycle off Purtan Island varied from 7.16 parts per thousand to 11.04 parts per thousand. On this day the highest salinity occurred one-half hour after high water and the lowest one-half hour after low water.

Figure 19 shows the data of tidal studies made at Yorktown on April 23, 1937. It is difficult to place the time of highest salinity in relation to time of high water in this series. The observations were started at high water in the morning and continued to high water in the evening. The salinity was decreasing at the time of the start of observations and was increasing when the measurements were ended. The lowest salinity occurred about 1½ hours after low water on the bottom and 2 hours after low water at the surface. The range of salinity at Yorktown during this tidal cycle was from 15.61 parts per thousand to 17.45 parts per thousand for the surface samples and from 15.68 to 18.51 parts per thousand for the bottom samples.

The results of tidal studies at Bell Rock Lighthouse on May 20, 1937, are presented in figure 20. The greatest salinity occurred one-half hour after high water and the lowest salinity occurred 1¾ hours after low water. The surface salinity varied from 3.91 to 7.41 parts per thousand and the bottom salinity from 4.13 to 7.99 parts per thousand.

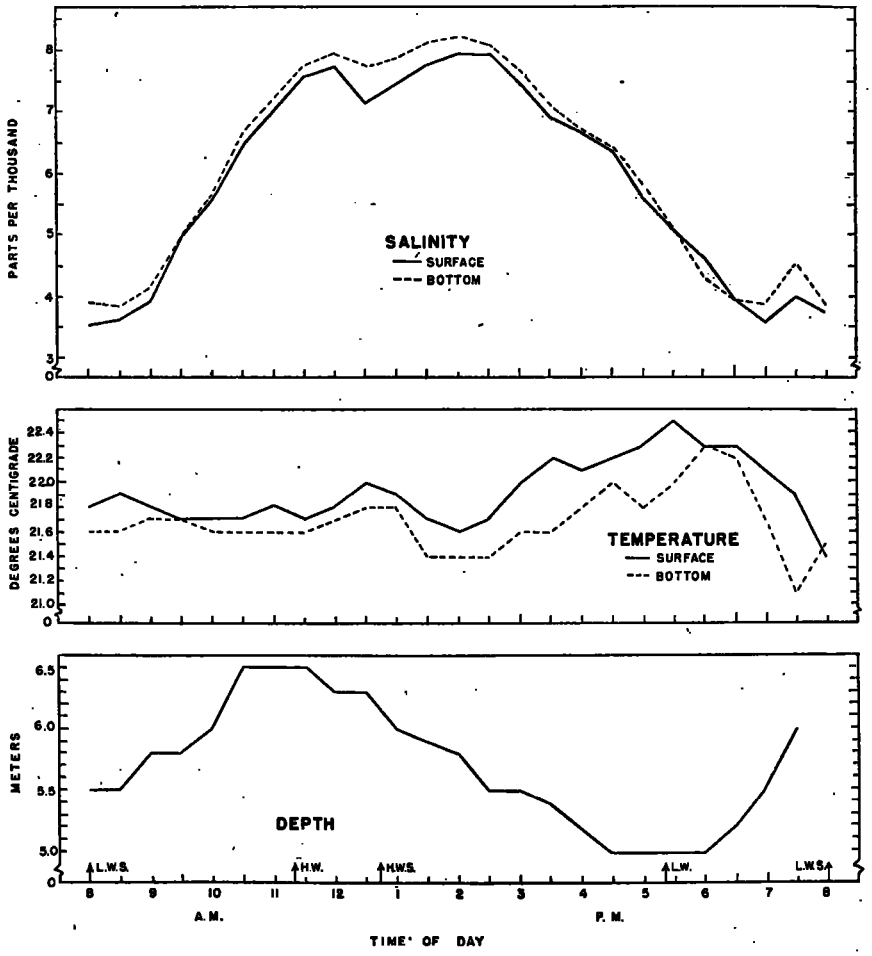

FIGURE 16.—Tidal changes in temperature and salinity of the water of the Pamunkey River at West Point on May 21, 1936. Arrows indicate stage of tide. L. W.—low water; L. W. S.—low water slack; H. W.—high water; H. W. S.—high water slack.

DISSOLVED OXYGEN

The dissolved oxygen content of the water of the York and Piankatank Rivers was determined for both surface and bottom samples at the different field stations at various times throughout the investigation.

The samples for the determination of oxygen were obtained with the Eckman water bottle. The water was then collected through a rubber tube extending to the bottom of a citrate bottle. Care was taken to have the tube full and to prevent aeration of the sample by bubbling. The dissolved oxygen content was determined by the Winkler (1888) method, as described by Kemmerer, Bovard, and Boreman (1923), and with the permanganate modification as given by the American Public Health Association (1933). The results were expressed in percentage of saturation, using the table of saturation of water with oxygen at various temperatures and salinities given by Whipple and Whipple (1911).

Despite the fact that the pulp-mill waste emptied into the York River at West Point has considerable oxygen demand, the dissolved oxygen content of the river was found to be not particularly low. At times during hot weather the oxygen of the water of the upper York does get rather low, but only rarely does it reach a figure critical to aquatic life. The Piankatank River was found to be relatively high in dissolved oxygen. The results of all observations at the various stations are presented in tables 21 and 22.

At times the water was found to be supersaturated with oxygen owing either to photosynthesis or to wave action. The latter has been responsible for most of the results showing a very high oxygen content.

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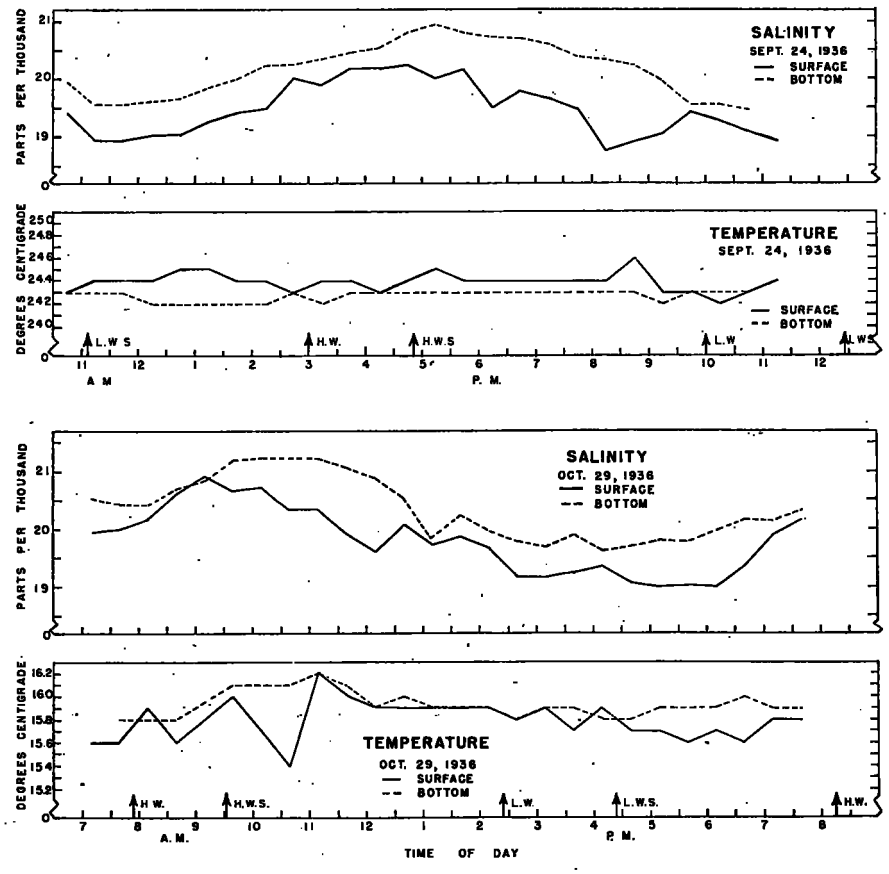

FIGURE 17.—Tidal changes in the temperature and salinity of the water of the York River at Yorktown on September 24 and October 29, 1936. Arrows indicate stage of tide. L. W.—low water; L. W. S.—low water slack; H. W.—high water; H. W. S.—high water slack.

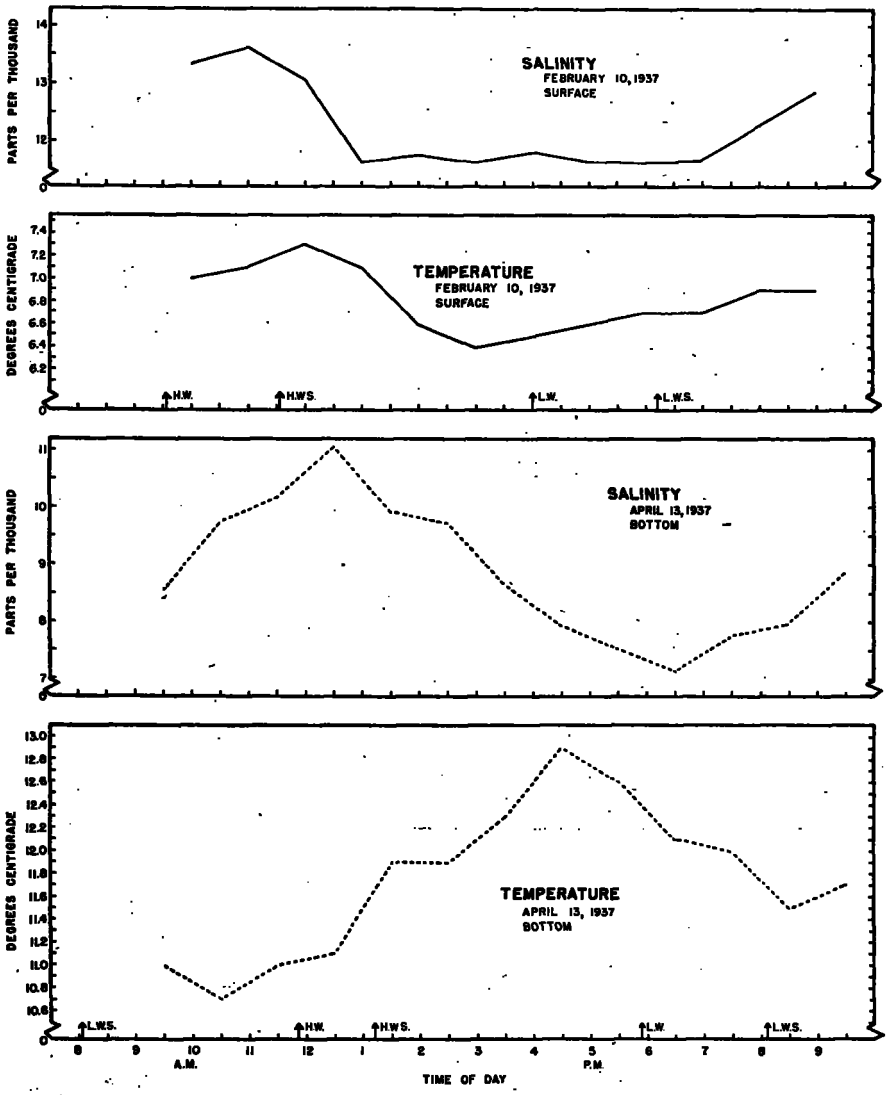

FIGURE 18.—Tidal changes in the temperature and salinity of the York River at Purtan Island on February 10 and April 13, 1937. Arrows indicate stage of tide. L. W.—low water; L. W. S.—low water slack; H. W.—high water; H. W. S.—high water slack.

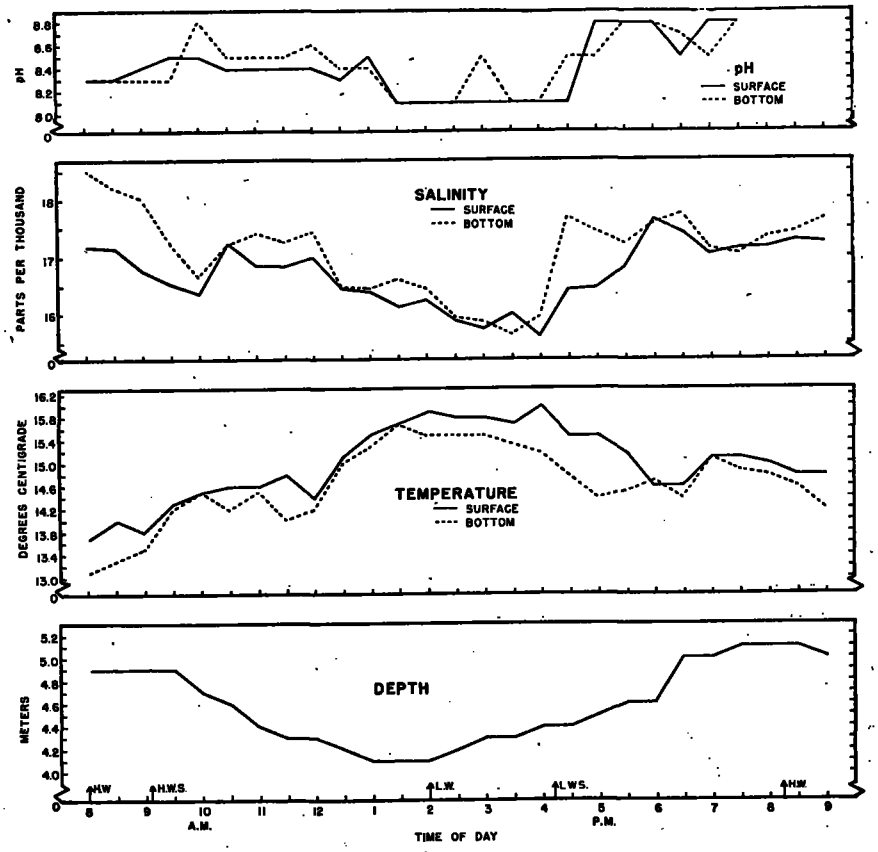

FIGURE 19.—Tidal changes in temperature, salinity, and hydrogen-ion concentration of the water of the York River at Yorktown on April 23, 1937. Arrows indicate stage of tide. L. W.—low water; L. W. S.—low water slack; H. W.—high water; H. W. S.—high water slack.

TABLE 21.—*Percentage of saturation of the water of the York River with dissolved oxygen*

Date	Stations																		
	20		14		15	23	5	22	6	16	17	8		9		18		19	
	Surface	Bottom	Surface	Bottom								Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
1935																			
Dec. 2			92.5	93.0	103.2														
Dec. 6	94.2	92.2					91.7			98.9	97.5								
Dec. 12	96.2	90.5	95.8	96.4	109.0		88.6												
Dec. 13										80.5				89.0	89.7	80.9	80.8	82.3	82.9
Dec. 23	110.8	96.8																	
1936																			
Jan. 3			96.8	97.4	97.6		94.1												
Jan. 4	95.1	94.1																	
Jan. 6																76.0	77.1	82.3	71.3
Jan. 7										95.3	87.7			88.8	90.3				
Feb. 19	94.5	93.9		93.4	90.8														
Feb. 20							95.0							87.9	86.0	87.1	87.1		
Feb. 21										88.3	87.4								
Feb. 27			96.6	85.6			93.5							85.2	72.3				
Mar. 16	101.2	104.7			104.7														
Mar. 18			103.5	109.0			101.1			100.6									
Mar. 19											73.8			80.2	86.2	55.1	52.7	86.1	85.7
Mar. 30	114.4	114.6			108.9		90.7			90.1									
Apr. 1											82.3			76.7	80.3	77.6	71.3	91.7	78.8
Apr. 14	99.7	96.5	92.3	100.0	94.9		89.1												
Apr. 16										92.6	100.8			94.3	106.8	87.1	99.2	94.0	103.5
Apr. 27				117.5	95.2		113.8												
Apr. 28										95.1		86.1	82.0	85.2	83.9	80.3	77.0	90.0	82.9
Apr. 29											108.3								
May 28	94.3				101.1														
June 1							107.0			101.7	109.4			114.9	108.7				

TABLE 21.—*Percentage of saturation of the water of the York River with dissolved oxygen*—Continued

Date	Stations																		
	20		14		15	23	5	22	6	16	17	8		9		18		19	
	Surface	Bottom	Surface	Bottom								Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
June 3																101.6	86.6	81.1	87.9
June 30	106.9	115.5		100.3	104.0		91.8												
July 2										76.0	84.5			97.1	87.1	78.3	72.3	83.8	76.8
July 27	110.2	101.1	109.2	107.6	108.3														
July 29						91.5	90.6	90.3	87.6										
July 31										66.9	77.9		78.2	83.4	57.2	89.4	78.4	86.7	64.4
Aug. 16											102.6		99.8	96.7	89.1	78.3	64.2	93.5	69.7
Aug. 26	105.3	101.0	86.8	87.4	82.0														
Aug. 28										85.0	89.8			59.0	62.3	95.6	83.3	76.8	77.0
Aug. 31						92.8	88.2	106.0											
Sept. 9				101.1	106.0	90.6													
Sept. 10							96.5	98.3	115.1	96.1	100.5								
Sept. 11													101.1	90.2	87.3	84.6	69.0	86.5	83.8
Sept. 14	84.8	88.4																	
Sept. 29			83.3	82.1	88.0	82.9	88.2												
Oct. 1								84.0					83.3						
Oct. 2	93.8	97.7							93.5	69.8	96.6			86.6	91.7				
Oct. 21	74.2	88.5	115.5	120.2	83.0	91.2	104.8	96.8	97.4	92.5	84.3								
Oct. 22												81.4	65.0	83.6	81.6	76.4	68.6	79.3	78.4
Nov. 4										83.3	88.2	85.5	82.9	81.4	76.8	75.1	74.9	84.4	83.4
Nov. 5				92.5	93.7	91.0	102.8	93.2	96.3										
Nov. 6	92.0	95.6																	
1937																			
Jan. 25	99.6	95.4																	
Jan. 26				87.9	90.8	89.1	87.3	85.5	86.4										
Jan. 27										83.6	84.7	84.7	81.1	74.8	70.6	57.7	54.7	62.8	68.8
Mar. 3										84.2	88.2	85.1	83.8	78.3	75.2	68.3	77.0	69.1	53.4
Mar. 4	101.8	94.8	91.7	92.4	98.1	96.3	96.0	94.8	93.1										
Mar. 30							99.4	100.0	91.3	98.5				96.9	95.3	95.0	89.4	91.5	89.6
Mar. 31	105.5	104.0	105.4	107.2	103.9	106.7													
Apr. 23			100.2	102.1	111.8	107.3	105.9	112.3	99.2										
Apr. 26	96.8	90.7																	
Apr. 27										90.9	107.9	87.3	81.7	84.5	77.9	71.1	75.0	75.5	70.6
May 17																65.8	65.3		
Average	99.1	97.7	97.7	98.6	98.8	93.9	96.0	96.1	95.5	88.5	92.2	85.0	83.9	86.4	83.6	79.1	75.2	83.2	78.3

TABLE 22.—*Percentage of saturation of the water of the Piankatank River with dissolved oxygen*

Date	Stations		
	55	53	
		Surface	Bottom
1935			
Dec. 10	101.4	97.4	100.7
1936			
Jan. 11	97.0	91.2	92.4
Mar. 3	108.6		99.4
Mar. 12	73.1	75.8	75.7
Apr. 3	102.9		97.8
Apr. 16	106.7		98.4
May 6	103.3	91.4	93.9
June 4	90.3	96.1	76.0
July 1	91.9		77.9
Aug. 3	87.7	79.8	82.6
Aug. 21	106.5	110.3	66.8
Sept. 3	96.0	100.4	101.6
Oct. 6	97.6	105.8	97.4
Oct. 26	96.4	92.6	94.0
Nov. 10	112.2	98.1	100.8
1937			
Feb. 2	99.2	86.7	78.0
Feb. 16	99.2	106.2	101.8
Apr. 6	113.6	105.3	105.0
Apr. 21	111.4	117.7	113.5
Average	99.7	97.0	92.3

Changes in the dissolved oxygen content of the water during a tidal cycle in the upper York River at Bell Rock Lighthouse on May 20, 1937, are shown in figure 20. It will be noted that fluctuations in the oxygen tension were following the time of day rather than the tidal cycle.

The horizontal distribution of dissolved oxygen in the water of the York River on the last of ebb tide on May 17, 1937, is shown in figure 21. It will be seen that there was less oxygen in the upper York than in the lower. The fact that the upper York was consistently lower in dissolved oxygen than the lower York can be seen from examination of figure 22, which shows the average percentage of saturation at the various stations.

Analysis of the data presented in table 21 shows a very definite decrease in the percentage of saturation from the mouth of the river (station 20) towards its head (stations 9 and 19). The annual mean values, which are more significant than single observations, show that in surface water samples, taken between these two points, the percentage of dissolved oxygen gradually decreases from 99.1 to 83.2. The figures for bottom samples, as one would expect, are lower, ranging at the same stations from 97.7 to 78.3 percent. For the Piankatank River the annual

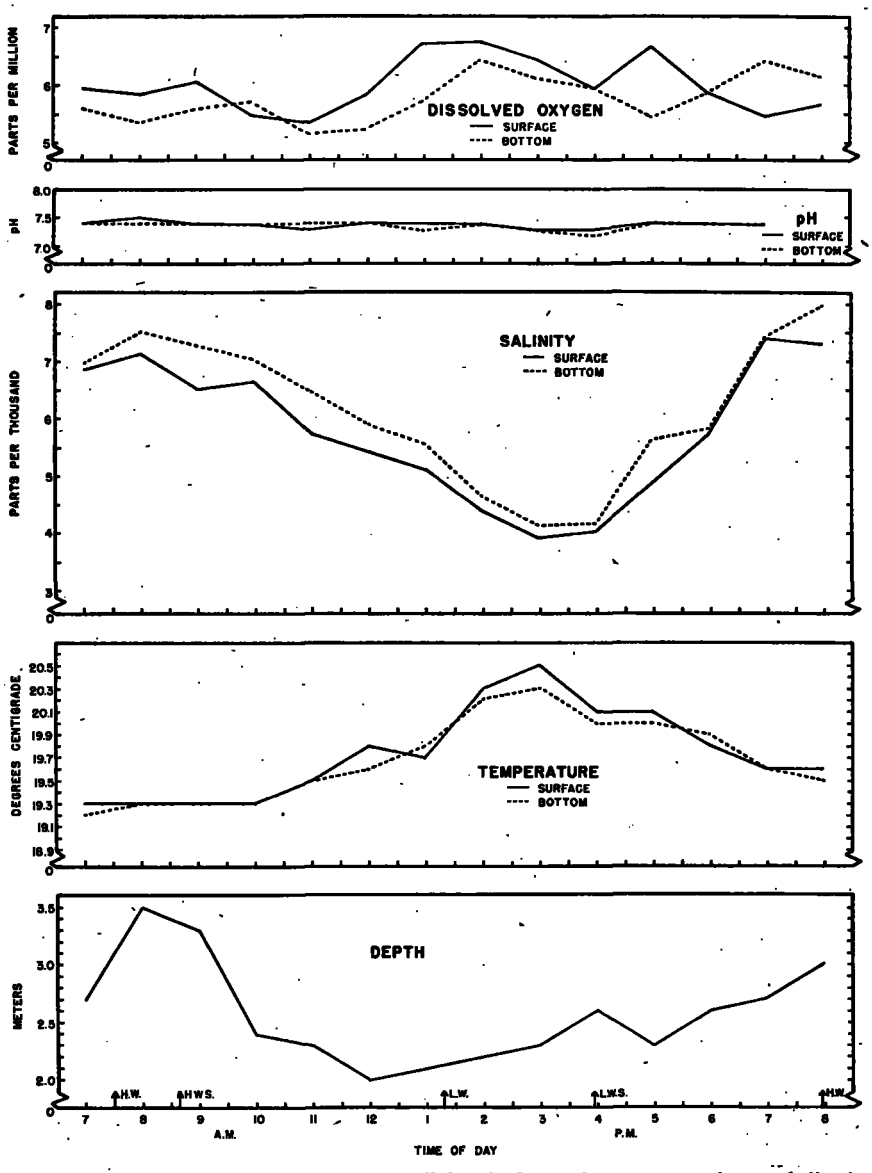

FIGURE 20.—Tidal changes in temperature, salinity, hydrogen-ion concentration, and dissolved oxygen of the water of the York River at Bell Rock Lighthouse on May 20, 1937. Arrows indicate stage of tide. L. W.—low water; L. W. S.—low water slack; H. W.—high water; H. W.S.—high water slack.

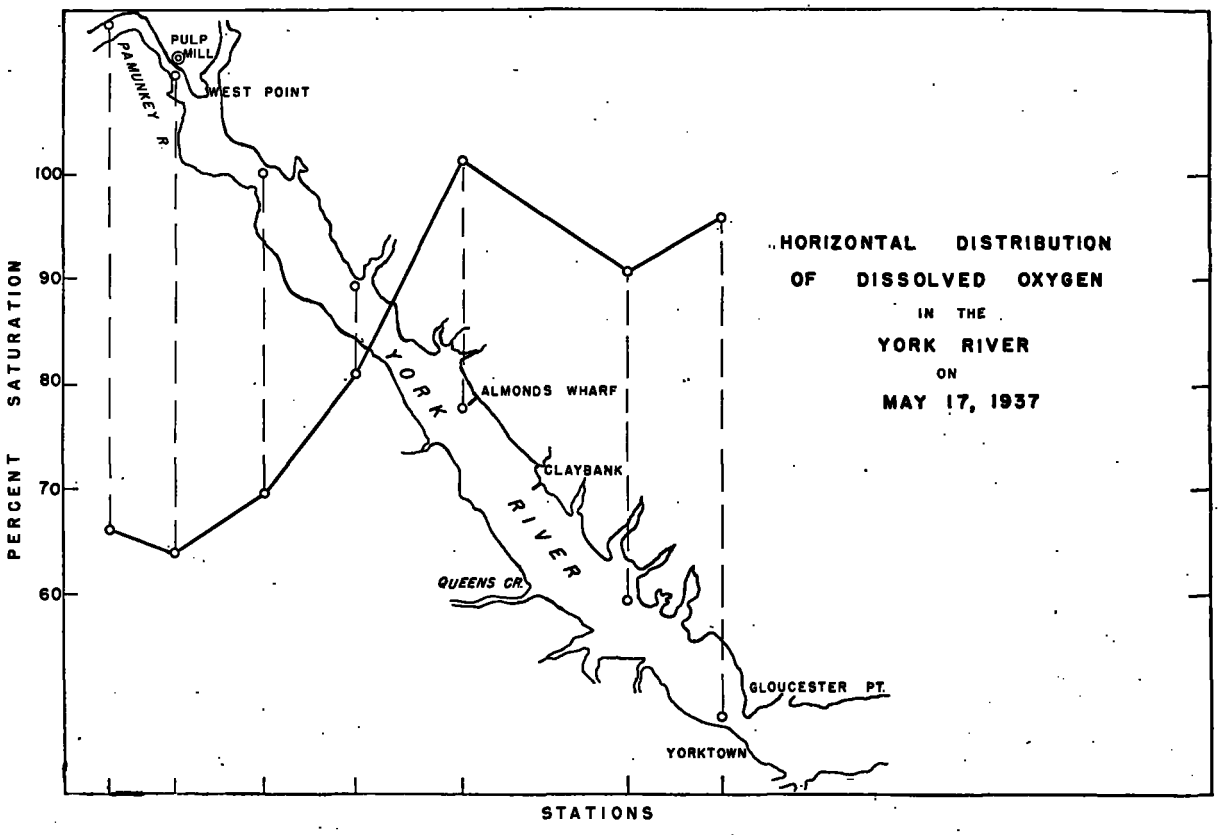

FIGURE 21.—Horizontal distribution of dissolved oxygen in the water of the York River on the last of ebb tide on May 17, 1937.

means vary between 99.7 and 97.0 percent for surface samples. The mean for bottom samples at station 53 is 92.3 percent.

HYDROGEN-ION CONCENTRATION

Samples of water collected at the various stations in the York and Piankatank Rivers were tested for their hydrogen-ion concentration, using Hellige comparator and standard indicators. In nearly all instances cresol red was used, but in a few cases brom-thymol blue was employed. The observed values were corrected for salt error according to the corrections given by Ramage and Miller (1925). The hydrogen-ion concentration of all water samples tested is given in terms of pH in tables 6–20 (pp. 177–186) and figures 13, 14, and 19.

The fluctuations in the pH of water were found to be rather extensive, varying from 6.9 to 8.4 in the York River and between 7.1 and 8.6 in the Piankatank. In both rivers there was a gradual decrease in the pH from the mouth to the head. This was due to the greater proportion of fresh water at the head of each stream. The lowest value, pH 6.9, was observed only once at the time of high water slack near West Point (station 9, February 20, 1936). The water was almost fresh having a salinity of only 0.86 part per thousand. Slightly acid water, pH 6.7 to 6.91, was encountered several times in the Mattaponi and Pamunkey rivers about 1½ or 1¾ miles above the bridge at West Point (tables 17 and 18).

As a general rule lower pH values occurred during times of freshets. Other seasonal and daily changes in the hydrogen-ion concentration were probably associated with the intensity of photosynthesis and other biochemical processes in the river.

PHOSPHORUS

Among the phytoplankton nutrients the phosphates feature importantly as the constituents of the sea water necessary for the growth of the algae. In this investigation biweekly samples of water were taken at various stations in the two rivers for phosphorus analysis. The cycle of phosphorus was followed from January 1936 to April 1937, using the

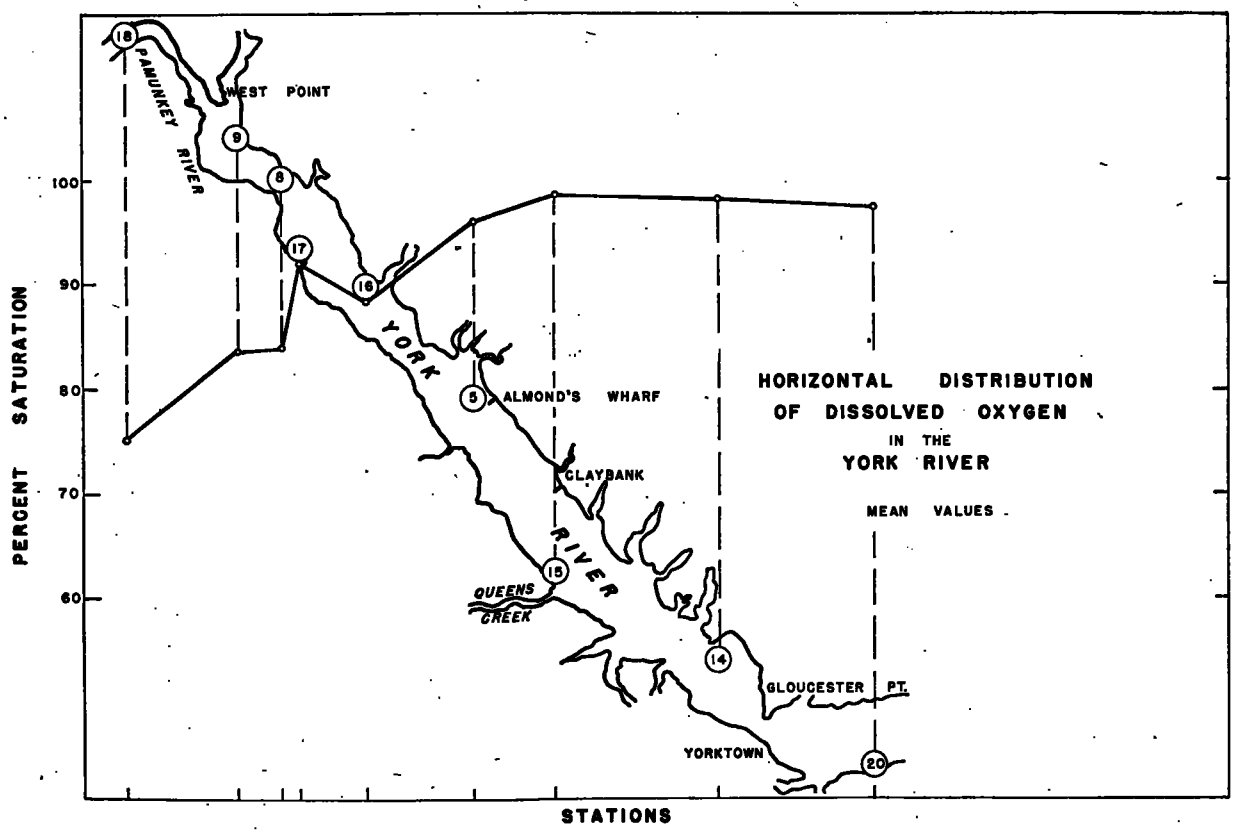

FIGURE 22.—Horizontal distribution of dissolved oxygen in the York River. Percentage of saturation based on mean values.

method of Atkins-Deniges as given by Seiwell (1935).

The results (given in tables 6 to 20)[3] show comparatively small quantities of phosphorus in the water of the two rivers. During the spring and summer months the quantities were negligible. In the fall and winter months the phosphorus content in the York River rarely reached 30 milligrams per cubic meter. Unexpectedly high content of 93 milligrams per cubic meter observed on January 27, 1937, at stations 8, 9, 16, 17, was of short duration, having disappeared within a fortnight.

Conditions similar to those found in the York River prevailed in the Pamunkey, Mattaponi, and Piankatank Rivers. Only on rare occasions did the phosphorus content reach 30 milligrams per cubic meter.

From these observations conclusions can be reached that fresh water entering these tributaries of the Chesapeake Bay contributes but very little to the supply of phosphates needed for the propagation of plankton.

[3] Tables 6 to 20 will be found on pp. 177–186

ACCUMULATION OF PULP-MILL EFFLUENT IN THE YORK RIVER

THE RATE OF DISCHARGE OF PULP-MILL EFFLUENTS AT WEST POINT

Determination of the total quantity of pulp-mill effluents discharged daily into the river at West Point was desired for evaluating the degree of pollution of the river and for computing the concentration of the pollutant in the river water. Unfortunately, no systematic records of the rate of flow of effluents in the various sewer outlets were available.

Observations had shown that the rate of flow, the appearance, and the specific gravity of pulp-mill effluents were subject to rapid and sudden changes depending on the various stages of operation of the mill. Since information on rates of flow was not available, observations were made on a number of occasions over sufficient periods to record these variations and to obtain data which would serve in evaluating the degree of pollution of the river and for computing the concentration of the pollutant in the river water. These observations are presented here with the necessary details for such computations.

Experimental data described (pp. 134–157) show that only the waste arising from the pulping process contained the physiologically active material in sufficient amount to demonstrate its effect within the limitations of the experiments. The following observations refer therefore only to the discharge of these effluents.

At the start of the investigation in the late fall of 1935, the visible sewer outlets at the mill were as follows:

1. A small ditch dug at the south end of the plant, draining the sludge pond located east of the mill and emptying into the river. The bottom of this ditch had an accumulation of gray sludge, which, from time to time, was cleaned by workmen. There was a small flow of a light brownish liquid in the ditch.
2. A ditch of considerable size leading to the river from a small pool located at the rear of the power plant and shops and which received the outlet of a number of pipes of various sizes. This ditch was lined with piling and completely covered over with planks. This pool and ditch carried considerable effluent of a moderately dark-brown color with small amounts of rather firm froth and at times contained some oil (fig. 4, A, B, C, D).
3. A large pipe with considerable flow emptying from a height of a few feet into the river at the south end of the lighter slip. This material appeared to be light yellow in color (fig. 4, E).
4. A large open ditch in back of the digester house running from the old pump house to the river. At the head of this ditch emptied a large tile pipe and a smaller cast-iron pipe. There was also a small ditch from the old board mill entering here. This small ditch had a very small flow of clear water. The large tile pipe carried a large flow of dark brown effluent and the smaller pipe carried some steam and water, also, large amounts of steam at the time of blowing a digester (figs. 4, J, H, I).

A blueprint received from an official of the plant showed the approximate lay-out of 10 sewer lines. The size of the sewers and their purpose was also listed and are given in the caption of figure 4. At this time, the rate of flow of the main sewers was given as follows: sewer *A*—200 gallons per minute; sewer *D*—150 gallons per minute; and sewers *J* and *H*—1,200 gallons per minute. These estimates were based on frequent observations which consisted in timing the travel of small wooden chips tossed into the sewers.

It was learned that early in 1936 an additional pipe (not shown in fig. 4) was installed leading from the weak-liquor storage tank to the head of the ditch leading from sewers *J* and *H*. This line carried off the foam that accumulated at the top of the tank. From observations made by the authors during the summer and fall of 1936 it was noted that this pipe ran black at times with a very alkaline, syrupy mixture and at other times was water-clear. The times of running black, however, were numerous and continued for long periods.

On April 7, April 20, and May 4, 1937, observations were made with a Price current meter on the rate of flow of effluent in the ditch leading from sewers *J* and *H*. A short distance down the ditch from its head a location was selected at which the flow was confined to a regular channel between well-defined banks and where the bottom was rather regular. It was observed that the greatest flow occurred at one place a little to one side of center. The current meter was placed in the swiftest current and the revolutions counted. The meter was then placed in the slowest current and the revolutions again counted. Observations were made at intervals of 10 to 15 minutes. At each time of reading of the current meter, the width of the flow was measured and the depth measured at three different locations in a line across the flow. From this information it was possible to compute the volume of effluent passing this point.

The rate of flow as measured by this means in the ditch leading from sewers *J* and *H*, for short periods, gave results of 400 gallons per minute on April 7; 642 gallons per minute on April 20; and 1,849 gallons per minute on May 4, 1937. The average flow computed from all these short periods of observation would be 990 gallons per minute.

During the early summer of 1937, wooden weirs were installed by the pulp mill in the ditch below sewers *J* and *H*, and in the ditch from the paper mill at the south end of the plant. These weirs were of sharp-crested rectangular form with end constrictions, the opening in the weirs being 36 inches by 12 inches. The volume of discharge was computed from measurements of the height of flow over the weir.

Observations made by the authors of the rate of flow at the wooden weir in the ditch below sewers *J* and *H* gave measurements averaging 1,031 gallons per minute on August 9; and 689 gallons per minute on September 1, 1937. At the latter date, the weir broke and observations ended. Because of the leaks around the weir causing the banks to give way, the readings for September 1 obviously are incorrect.

On January 18, 1938, representatives of the Chesapeake Corp., while visiting the Yorktown laboratory for the discussion of the progress of the investigation, stated that, according to observations made at the wooden weir by mill employees, the rate of flow in the ditch below sewers *J* and *H* averaged at that time 1,500 gallons per minute, or 2,160,000 gallons per day.

Considerable difficulty was experienced by the mill with these weirs as a result of the soft banks and

the leakage around the weirs. Large amounts of clay were added to the banks from time to time, but finally the weirs were discarded. The wooden weir in the ditch leading from the paper mill at the south end of the plant never proved satisfactory and insofar as is known, no readings were made that were of value.

On April 4, 1938, it was observed that well-constructed weirs of reinforced concrete were being built at the lower end of sewers *J* and *H*. Two weirs were installed in the ditch, the more southerly one receiving materials from the overflow pipe from the liquor-storage tanks and the blow-down line from the digesters, and the more northerly one receiving material from the large tile pipe *J* and *H*, mostly wash waters from the diffusers. Automatic samplers were installed consisting of a hollow arm rotated by an electric motor. This arm, with a cup on the end, picks up a sample and delivers it through the hollow tube to a small storage tank. A float connected to a recording arm makes a record of the height of the liquid in the weirs. Only the sampler of the north weir was in operation. The flow of the other weir was not measured and no samples were taken. A shower spray of fresh water kept down the foam on the top of the weirs.

On October 13, 1938, it was learned from the plant chemist that, beginning sometime the first part of the year, an excess of salt water from the condensers had been added to the flow in weirs *J* and *H*. This was added irregularly, some shifts adding it and others not. It was added sometimes for days at a time and at other times not added at all for a week. When salt water was added, the flow was nearly doubled. According to a plant official, the rates of flow obtained during six hour shifts averaged 500 gallons per minute when the salt water was not added and 833 gallons per minute when it was added.

Subsequent changes in the sewer lines have been made by the pulp-mill company with the view of conserving water. Certain effluents, such as part of the waste water from diffuser washings formerly emptied into sewers *J* and *H*, were now utilized for washing logs in the barking drums and hence entered the river from other outlets. It was also noticed that the pipe from the black-liquor-storage tanks did not carry so much heavy material into the weir as formerly.

While collecting samples on December 9, 1938, it was observed that the small ditch from the old board mill (fig. 4) carried a considerable flow of a dark-brown effluent with much fiber. Hitherto, this ditch had only a small flow of clear water. On tracing back it was found that this material was entering the ditch from a hole in the side about half way to the old board mill. The ditch above this point had a very small flow of clear water.

During the late fall of 1938 the ditch below sewers *J* and *H* leading to the river was filled in and a new ditch was dug, reinforced with pilings, and completely covered with planks. The new ditch emptied into the barge slip beyond the barking drums (fig. 4, No. 7).

No measurements of rate of flow were made by the authors using the new concrete weir. It was learned from one of the assistants to the plant chemist in January 1939 that the rate of flow in the weir receiving the effluent of sewers *J* and *H* averaged 2,500,000 gallons per 24 hours (1,736 gallons per minute) and that the flow originated in the screening building and in the evaporator house (fig. 4, Nos. 3 and 9).

TABLE 23.—*Rate of flow in ditch below sewers J and H and specific gravities of effluents as observed on Apr. 7, Apr. 20, and May 4, 1937*

Time of day	Cross section area in square inches	Rate of flow		Specific gravity of effluents at 17.5°C.
		Feet per second	Gallons per minute	
APRIL 7				
3:40 p. m.	193.5	0.51	308	1.0027
3:50 p. m.	193.5	.71	428	1.0021
4:00 p. m.	193.5	.61	368	1.0065
4:00 p. m.	193.5	.65	392	1.0025
4:20 p. m.	258.0	.66	398	1.0014
4:30 p. m.	258.0	.92	740	1.0041
4:40 p. m.	258.0	.62	499	----------
4:50 p. m.	301.0	.35	328	----------
5:00 p. m.	344.0	.27	136	----------
Mean	----------	----------	400	----------
APRIL 20				
2:40 p. m.	236.5	0.45	372	1.0049
2:58 p. m.	215.0	1.19	798	1.0013
3:10 p. m.	193.5	.70	422	1.0066
3:20 p. m.	236.5	.54	446	1.0023
3:30 p. m.	236.5	.75	620	1.0048
3:45 p. m.	215.0	.58	389	1.0032
3:55 p. m.	279.5	1.62	1,412	1.0032
4:35 p. m.	387	.58	675	1.0042
Mean	----------	----------	642	----------
MAY 4				
1:20 p. m.	427.2	1.53	2,252	1.0027
1:30 p. m.	472.3	1.77	2,618	1.0029
1:40 p. m.	404.9	1.16	1,463	1.0029
1:50 p. m.	495.0	1.49	2,300	1.0025
2:00 p. m.	495.0	.91	1,405	1.0044
2:10 p. m.	----------	----------	----------	1.0031
2:20 p. m.	676.0	.50	1,054	1.0055
Mean	----------	----------	1,849	----------

As many changes were made in the arrangement of the sewer outlets from time to time, and the wooden weirs constructed did not prove satisfactory and often washed out, the authors employed for their calculations only the observations which they made personally by using the current meter. The data of the rate of discharge through sewers *G* and *H* are summarized in table 23.

For the computation of the concentration of the effluent the mean of the three series observations reported in table 23 were used. The estimated rate of influx of this effluent of 963.6 gallons per minute appears to be conservative compared to others obtained at different times by the authors and by pulp-mill representatives. Converting it into feet per acre the value of 4.26 feet per acre per day is obtained. This value has been used in the subsequent computations.

CONCENTRATION OF THE PULP-MILL EFFLUENT IN THE TIDAL WATERS OF THE YORK RIVER

If the material discharged by the pulp mill is stable and is not immediately destroyed by river water, one would expect that a steady influx of it over a period of several years would result in building up a definite concentration in a tidal basin. Since the rate of destruction of the effluent in the river is not known and no chemical method is available at present for its quantitative determination, we must consider a theoretical case, assuming first that there is no destruction of the effluent and that the effluent is thoroughly mixed and is uniformly distributed in the cross-sectional area of the stream. Under these conditions the dilution of the effluent over the oyster grounds would depend on two variable factors, namely, the rate of its discharge by the pulp mill, and the river flow. The resulting concentration of the pollutant and the time required for reaching an equilibrium can be computed.

It has been shown above that 4.26 acre-feet per day may be considered a conservative rate at which a physiologically active pulp-mill effluent is discharged into the head of York River at West Point.

From the observation on currents at the cross-sectioned area of the River opposite Purtan Island, described in detail on pages 72–78, it has been determined that the influx of tidal water into the river basin is equal to 11,054.54 acre-feet per day.

An estimate of the volume of the river basin is available from the data of Brown, Seavy, and Rittenhouse, published in the Report on Investigation of Silting in the York River (1939). Table 1 of this report gives estimates of the water volume of the river of 222,189 acre-feet in 1911 and 206,896 acre-feet in 1938. For the purpose of the present work the middle value of the two figures, namely 214,542 acre-feet, has been used. In determining the volume of water in the York River, Brown, Seavy, and Rittenhouse (loc. cit.) obtained the cross-sectional areas of water below mean low water and measured the corresponding surface by planimeter using the United States Coast and Geodetic Survey Chart No. 495, published in 1931. From these data the volume of water was calculated for each segment by using Dobson's formula for reservoir capacities (Dobson 1936). The length of the York River was divided into 12 segments shown in figure 23 which represents a reproduction of the Sedimentation Survey chart. Unpublished data received from the Soil Conservation Service give the water capacities for each segment separately (table 24). If the two lower segments (11 and 12, figure 23), located in the part of the river in which the oysters are not affected by pollution, are excluded, the volume of that part of the river in which oysters show abnormal symptoms (segments 1–10 inclusive) can be estimated as equal to 131,411 acre-feet.

The proportion of the pulp-mill effluent in the river basin can be calculated by using the formula suggested by Prof. H. Hotelling, then of Stanford University, and employed in the studies conducted by the former United States Bureau of Fisheries on the effect of red liquor (waste from the sulfite pulp-mill process) on Olympia oysters, *Ostrea lurida* (Hopkins, Galtsoff, and MacMillin, 1931, 183–184).

TABLE 24.—*Water capacity of various segments of the York River, determined by the sedimentation survey of Oct. 25 to Nov. 25, 1938, made by the Soil Conservation Service, U. S. Department of Agriculture*

Bounding ranges	Water capacity	Surface area
	Acre-feet	*Acres*
6–7	7,898	1,079
7–8	9,746	1,288
8–9	9,133	995
9–10	9,553	1,216
10–11	11,717	1,578
11–12	18,816	2,157
12–13	12,634	1,216
13–14	15,516	1,576
14–15	15,131	1,635
15–17	21,267	2,145
17–18	21,614	2,030
18–19	53,871	4,748
Total	206,896	21,663

According to Hotelling's formula—

$$p=\frac{a}{a+b}\left[1-\left(1-\frac{a+b}{V}\right)^t\right]$$

where p—is the proportion of pulp mill effluent in basin
a—the rate of discharge of pulp mill effluent in acre-feet per day
b—the rate of influx of water into the basin in acre-feet per day
V—total volume of the river basin
t—time in days since the pollution started.

The problem of computing the concentration of pulp-mill effluent in the York River was presented this time to Dr. L. B. Tuckerman, Assistant Chief, Mechanics and Sound Division, National Bureau of Standards, who was kind enough to prepare a memorandum which is quoted in part.

Let a=rate of discharge of poisonous pulp liquor at the pulp mill in acre-feet per day
b=the rate of influx of water into the river basin in acre-feet per day. This includes the influx of water from the river above the mill and the daily influx of tidal water
V=total volume of the river basin
p=proportion of poisonous pulp liquor in bay
p_∞=limit which proportion of poisonous pulp liquor in bay approaches after a long time
t=time in days since the pollution started.

Assuming that these processes are continuous and that the mixing of the poisonous liquor with the water of the bay is practically instantaneous the daily efflux of poisonous liquor from the bay will be equal to $p\,(a+b)$ so that the total rate at which the poisonous liquor increases in the bay is:

$$\frac{d(pV)}{dt}=a-p(a+b)$$

which gives the linear differential equation for p as

$$\frac{dp}{dt}+\frac{a+b}{V}p=\frac{a}{V}$$

The solution of this differential equation under the terminal condition

$$p_{t=0}=0$$

readily is found to be:

$$p=p_\infty(1-e^{-kt})$$

where

$$p_\infty=\frac{a}{a+b},\text{ and } k=\frac{a+b}{V}$$

The difference between this solution and the solution

$$p=\frac{a}{a+b}\left[1-\left(1-\frac{a+b}{V}\right)^t\right]=p_\infty[1-(1-k)^t]$$

given by Hotelling, lies in the fact that in this solution the influx of poisonous liquor and water and the efflux of the mixed fluid of concentration, p, are assumed to be continuous while Hotelling assumes that the influx and efflux occurs discontinuously once a day. These two solutions indicate the same value for the limiting value of p

$$p_\infty=\frac{a}{a+b}$$

but differ in the rate at which this limit is approached. However, for small enough values of $k=\frac{a+b}{V}$ these two rates are practically identical, since

$$e^{-k}=(1-k)+\tfrac{1}{2}k^2-\tfrac{1}{6}k^3+\ \ldots$$

and if k is small enough the terms

$$\tfrac{1}{2}k^2-\tfrac{1}{6}k^3+\ \ldots$$

make little difference.

The maximum difference between the concentration calculated from the two formulas will occur at a time given by

$$t=\frac{\log\,[\log\,(1-k)/\log\,e^{-k}]}{\log\,[e^{-k}/(1-k)]}$$

or approximately for k small in comparison with 1,

$$t=\frac{1}{k}(1-\tfrac{1}{4}k+\ \ldots)$$

If a=4.26 acre-feet per day, b=11053.54 acre-feet per day, and

$$V=214542 \text{ acre-feet}$$

$$k=\frac{a+b}{V}=0.05154$$

$$1-k=0.94846$$

$$\text{and } e^{-k}=0.94976$$

For these data the maximum difference between the concentrations calculated by the two formulas will then occur at about

$$t=\frac{1}{0.05154}(1-0.0129)=19.2 \text{ days.}$$

This was checked by computing $(1-k)^t$ and e^{-kt} and their difference for t=19.0, 19.2 and 19.4 days.

t Days	$(1-k)^t$	e^{-kt}	$(1-k)^t-e^{-kt}$
19.0	.63411130	.62442122	.00969008
19.2	.63796324	.62827291	.00969033
19.4	.64177463	.63208510	.00968953

The computations were carried to 8 decimal places since over this range the difference was constant to 6 decimal places. These results show clearly the existence of a maximum difference between the two formulas of less than 1 percent in the neighborhood of t=19.2 days.

In view of the broad assumptions made in formulating the problem this difference is wholly insignificant. Since Hotelling's formula uses somewhat simpler calculations, it is to be preferred if estimates are to be made upon assumptions such as those used here.

Either formula gives for the final concentration

$$p_\infty=\frac{a}{a+b}=\frac{4.26}{11057.8}=0.000385$$

Below are calculated by Hotelling's formula the values of

$$\frac{p}{p_\infty}=1-(1-k)^t$$

for a number of days up to 100:

t Days	$\frac{p}{p_\infty}=1-(1-k)^t$
1	0.052
2	.100
3	.147
4	.191
5	.232
6	.272
7	.310
8	.345
9	.379
10	.411
15	.548
20	.653
25	.734
30	.796
35	.843
40	.880
45	.908
50	.929
60	.958
70	.975
80	.985
90	.991
100	.995

The formula $\frac{p}{p_\infty}=1-e^{-kt}$ would give 0.990 for 90 days and 0.994 for 100 days which emphasizes again how little choice there is between the two formulas. As can be seen the final limit of $p_\infty=0.000385$ is practically (within 1 percent) reached in 90 days after the start of the pollution.

These assumptions are of course inadequate to give any picture of the decrease of pollution with increasing distance down the bay from the mill.

There seems to be no reasonable way to attack this problem so long as the concentration at any station is assumed to vary with the time. However, after a relatively short time, say 100 days, compared with the total time of pollution, several years, it may be assumed that at each station along the river a practically steady regime has been reached. Some idea of the law, but not the magnitude of that decrease, may then be gained from the following further assumptions.

Assume that p has reached its limiting value $p_\infty=\frac{a}{a+b}$ throughout the basin. Assume further that the flow of fluid down the basin is uniform across the stream bed. Then the time required for any given volume of polluted water to flow from the mill to any lower station will be proportional to the total volume, v, of water lying between that station and the mill, i. e., $t=cv$, where c is some constant.

If it is further assumed that there is some process acting which removes or destroys the poisonous constituents in any given portion of the poisoned water at a certain rate per day, the poisonous effect of the water at any station in the basin may be represented by πp_∞, where π is the fraction of the poisonous constituent which has not yet been removed or destroyed at that station. Since the regime is assumed to be steady

$$\frac{\partial\pi}{\partial t}=0$$

and

$$\frac{d\pi}{dt}=\frac{\partial\pi}{\partial t}+\frac{\partial\pi}{\partial v}\frac{dv}{dt}$$

reduces to

$$c\frac{\partial\pi}{\partial v}=\frac{d\pi}{dt}$$

Two different assumptions as to the rate of removal or destruction of the poisonous constituents suggest themselves.

1. The time rate of decrease of the concentration of the poisonous effect at any station

$$\frac{\partial\pi p_\infty}{\partial t}=-c'$$

is a negative constant (a constant rate, c', of supply of the removing or destroying agent).

2. The time rate of decrease of the concentration of poisonous character at any station

$$\frac{\partial\pi p_\infty}{\partial t}=c''\pi p_\infty$$

is proportional to its concentration (a monomolecular reaction).

The first assumption leads to the equation

$$\frac{\partial\pi}{\partial v}=-cc'$$

where c' is some other constant.

This gives $\pi=1-cc'v$

so that below a certain station given by

$$v=\frac{1}{cc'}$$

the water will be wholly innocuous.

The second assumption leads to the equation

$$\frac{\partial\pi}{\partial v}=-cc''\pi$$

which gives

$$\pi=e^{-cc''v}$$

where c'' is still another constant.

According to this the poisonous effect will diminish exponentially with volume of water between the station and the mill but will be present to some extent throughout the whole basin and out into the bay beyond.

Dr. Tuckerman's computations show two important facts: first, that at the rate of discharge of 4.26 acre-feet per day the final concentration is about 0.0004. This figure is very close to the threshold concentrations observed in laboratory tests (see pp. 134–157) which showed that pulp-mill effluent is physiologically effective in the concentration between 1:1000 and 1:2000. It is significant that the concentration computed on a theoretical basis is of the same degree

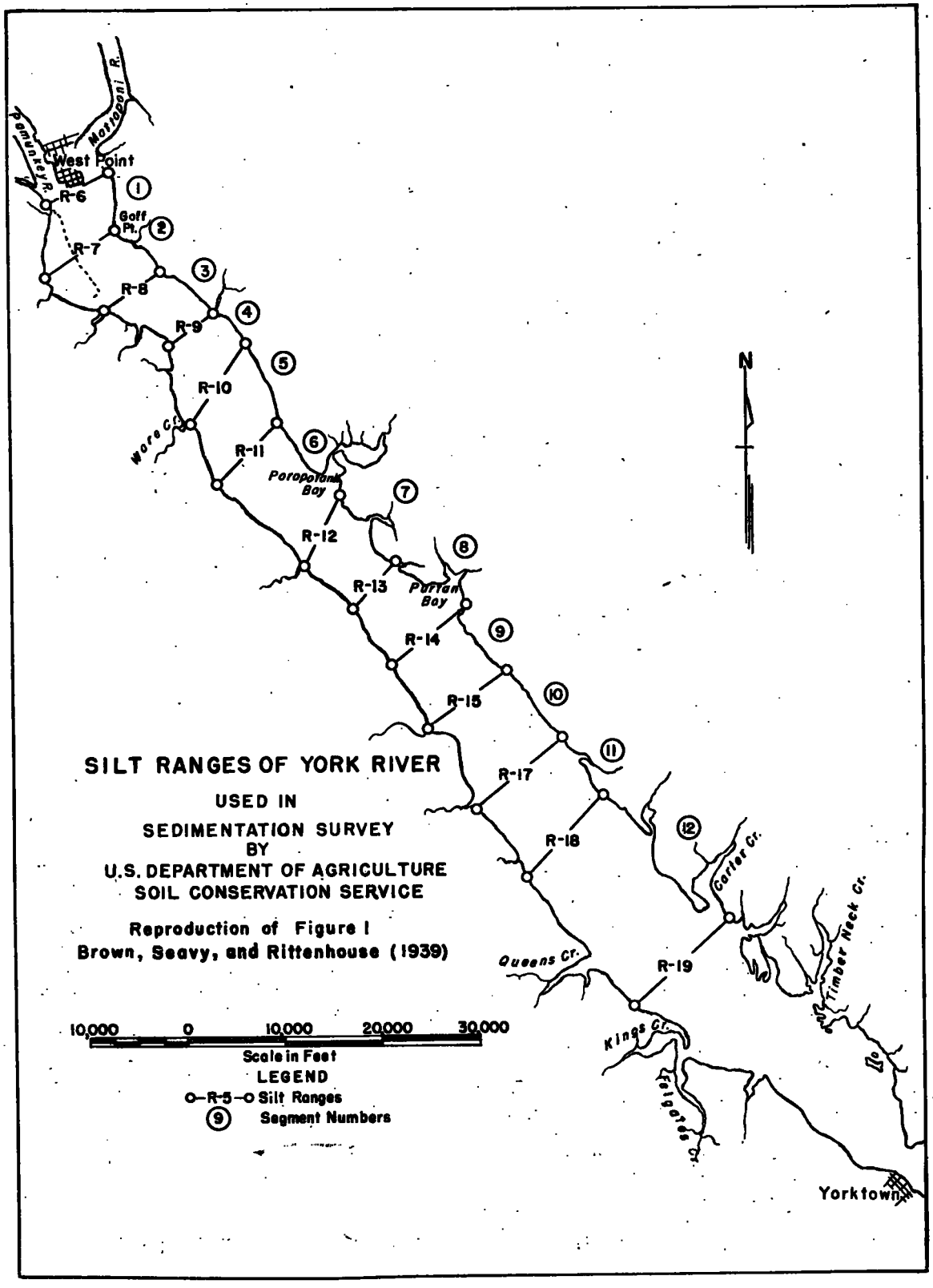

FIGURE 23.—Silt ranges of York River used in sedimentation survey by Soil Conservation Service, United States Department of Agriculture. Reproduction of figure 1 of the report by Brown, Seavy, and Rittenhouse (1939).

of magnitude as the physiologically effective concentration determined experimentally. It can be easily seen that with the slightly increased rate of discharge of about 1,500 gallons per minute or 6.63 acre-feet per day[4] which has been frequently recorded by the pulp-mill officials, the final concentration in the river equals 0.0006 or 1:1666.

The second important conclusion revealed by the computations is that, assuming there is no destruction of the effluent, the equilibrium is reached in about 90 days after the beginning of the pollution. If we consider only the upper two-thirds of the river basin, the volume of which is 131,411 instead of 214,542 acre-feet used in the computation, the final concentration, $p=\frac{a}{a+b}$ will be reached in a correspondingly shorter time.

Dr. Tuckerman's suggestion that the toxic effect will diminish exponentially with the volume of water between the source of pollution and a given point along the river is very valuable for further research. Condition of oysters in the York River clearly show that at present no toxic effect is noticeable in the lower part of the river.

PLANKTON CONTENT OF THE YORK AND PIANKATANK RIVERS

A study of seasonal changes in the plankton content of the waters of the York and the Piankatank Rivers was especially pertinent as there was the possibility that a scarcity of available oyster food might be responsible for the poor condition of the oysters in the upper York River.

By means of a Birge-Juday plankton trap biweekly samples were obtained of the surface water (0.5 meter) overlying oyster bottoms at stations 20, 14, 5, 16, 17, and 9 in the York River, and 55 and 53 in the Piankatank River. At stations 20, 14, 9, and 53, where the depth was greater than 2 meters, a sample of water just off the bottom was also taken.

Two liters of the water sample were passed through a Foerst-Juday centrifuge rotating at 20,000 revolutions per minute. The centrifugate was then transferred to a 15-millimeter tube, and centrifuged for 5 minutes in a clinical centrifuge. The water was decanted and 10 milliliters of 80-percent acetone added to the sediment in the bottom of the tube. After shaking, the tube was set aside for 15 minutes for extraction of the green coloring matter and was then again centrifuged for another 5 minutes. Comparison of the color was then made with the Harvey (1934) standards of nickel sulfate and potassium chromate, and the results expressed in pigment units per liter of original sample. Each unit was equivalent to approximately 10,000 organisms (diatoms and dinoflagellates).

In addition, 500 milliliters of the sample were likewise centrifuged and the sediment preserved in vials with formalin for identification and counting.

The reliability of Harvey's method has been checked by the authors by comparing the values of the pigment units with the total number of diatoms and dinoflagellates found in the same sample. The results, plotted in figure 24, show that in general the two curves follow the same trend and with the exception of the first observation (February 1936) are in agreement. As we may expect, the pigment unit curve is less jagged than the curve of the total number of forms. The pigment unit technique is, therefore, very useful in following the seasonal fluctuation in the abundance of phytoplankton. It cannot be used, however, in case it is necessary to determine the amount of living matter produced in the form of plankton.

Results of the observations of the amount of plankton present at the various stations are given in table 23. The averages for the entire period have been plotted on the maps in figure 25.

Mean plankton content in the York River computed from all the observations was equivalent to 48.7 pigment units as compared with 31.9 units in the Piankatank. The means computed separately for the lower and upper parts of the York River (table 25) are 47.4 and 50.0, respectively. Obviously, the difference between the plankton production in the lower and upper parts of the river is insignificant. A comparison with the Piankatank River, which is known to produce good oysters, shows that there is no deficiency in the phytoplankton productivity in the York River. Evidence from plankton studies points rather to an opposite direction suggesting that the potential supply of plankton is more abundant in the York River than in the Piankatank, where the annual mean of pigment units per liter was 31.9

A study of the seasonal distribution of plankton at different stations (table 25) shows that throughout the major part of the year the upper part of the York River was slightly richer in plankton than the

[4] One acre-foot equals 325,851 gallons.

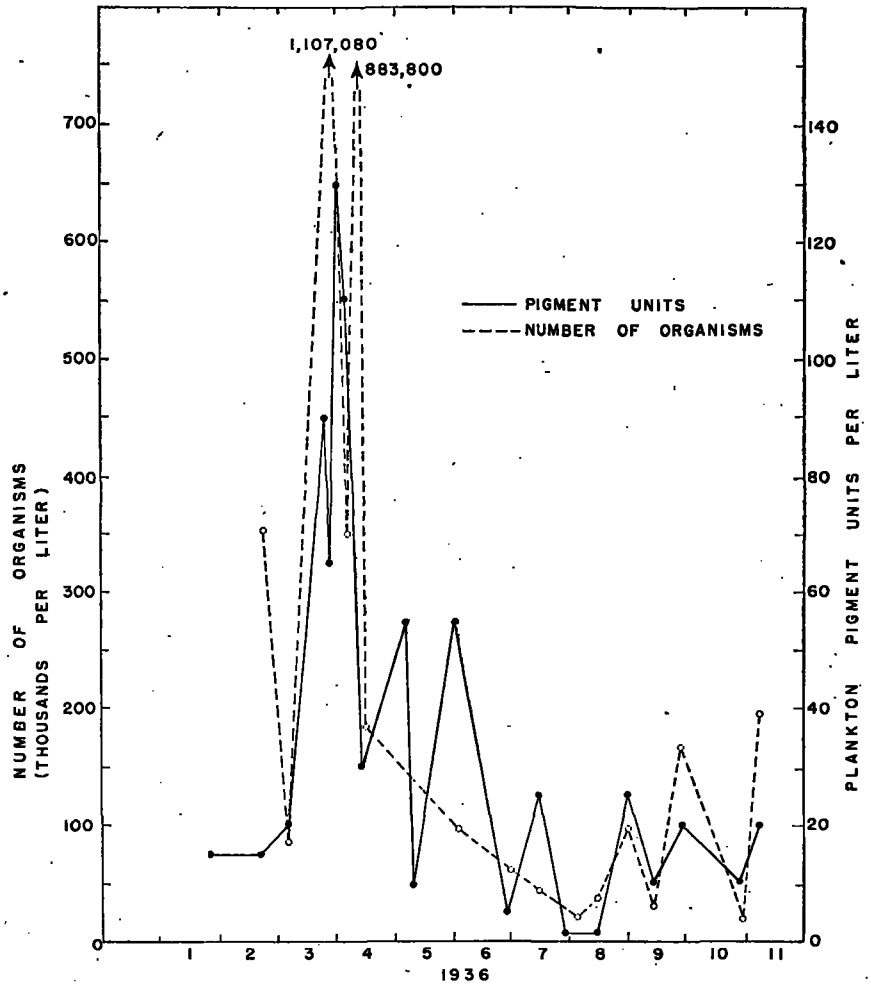

FIGURE 24.—Comparison of the results of counting, using the plant-pigment method for quantitative determination of the plankton in the York River, 1936.

lower part. Station 17 in the upper part of the river was especially rich in plankton. In April 1937 the plankton content reached here the highest mark of 240 units, equivalent to over 2 million organisms per liter. Such a density of phytoplankton has not been encountered at other stations.

A comparison of the cyclic changes in the plankton crop based on pigment unit determinations at stations in the York and Piankatank Rivers is presented in figure 26. It was found that in both rivers the maximum occurred at the usual vernal period, March to April. Slight increases noted in July, August, November, and December were insignificant in comparison with the spring maxima. Throughout the summer the amount of plankton remained relatively low. The increased spring production of plankton in the York River occurred between temperatures of 8° to 16° C. in 1936, and the amount of plankton decreased rapidly after the temperature rose above 16° C. During the spring of 1937 the maximum was likewise reached at a temperature of 8° C. In the Piankatank River the same situation was recorded, the maximum vernal crop having occurred at 8° C. in 1936 and at 13° C. in 1937.

The results of counting the predominant forms in phytoplankton samples collected from December 1935 to November 1936 at stations 20 and 17 in York River are shown in tables 26 and 27. The genus *Nitzschia* exceeded any group of diatoms in the river but was not the most abundant organism throughout the year, for the summer months brought the genus *Rhizosolenia* to the maximum at station 20, while *Thalassiothrix* was most abundant during the summer at station 17. With the exception of

TABLE 25.—*Plankton pigment units per liter of water in the York and Piankatank Rivers.*

[Stations 20, 14, 15 are located in the lower part of the river; stations 5, 16, 17, and 9, in its upper part]

Date	York River									Piankatank River		
	Stations in lower part				Stations in upper part							
	20	14	15	Mean	5	16	17	9	Mean	55	53	Mean
1936												
Jan. 21–23	11	17	11	13.0	15	18	15	10	14.5			
Feb. 19–20	90	30	55	58.3	15	50	42	30	34.3			
Mar. 4–6	36	30	25	30.3	20	24	140	22	51.5	16	22	19.0
Mar. 23–25	110	20	52	60.7	65	85	200	65	103.8			
Mar. 30–Apr. 1	30		130	80.0	130	130	165	65	122.5	38	55	46.5
Apr. 8–9	70	100	200	123.3	110	50	50	45	63.3			
Apr. 14–16	24	100	190	104.7	30	65	55	24	43.5	70	110	90.0
Apr. 27–May 1	200	20	75	98.3	50	65	120	30	66.2	10	10	10.0
May 12–14	10	10	10	10.0	10	75	100	52	59.2			
June 1–3	10	10	28	16.0	55	55	75	10	48.7	10	10	10.0
June 16–19		32		32.0		5	65	42	37.3	10	12	11.0
June 30–July 2	5	5	5	5.0	5	27	42	10	21.0	5	10	7.5
July 15–18	20	5		12.5	25	60	45	28	39.5	0	18	9.0
July 27–31	0	5		2.5	35	45	70	50	50.0	10	16	13.0
August 14–17	15	5	28	16.0	0	0	55	37	23.0	5	5	5.0
August 26–31	10	10	16	12.0	25	18	28	15	21.5	10	14	12.0
Sept. 9–14	12	12	80	34.7	10	10	10	17	11.7			
Sept. 29–Oct. 1	15	35	20	23.3	5	22	25	20	18.0	10	15	12.5
Oct. 20–22	15	15	15	15.0	10	25	35	24	23.5	32	20	26.0
Nov. 4–6	0	50	80	43.3	20			25	22.5	10	15	12.5
Nov. 20–24	18	12	45	25.0	15	35	25	35	27.5	18	25	21.5
Dec. 3–9	10	25	50	28.3	25	32	25	22	26.0			
Dec. 14–23	17	10	20	15.7	20	30	45	40	33.8			
1937												
Jan. 4–8	10	15	160	61.7	40	60	45	45	47.5	20	25	22.5
Jan. 25–27	22	17	65	34.7	25	30	30	15	25.0	15	60	37.5
Feb. 11–16	16	20	37	24.3	45	45	37	37	41.0	37	50	43.5
Mar. 3–4	20	30	37	29.0	7	60	60	20	44.2	40	45	42.5
Mar. 22–23	100	90	140	110.0	120				(120.0)	100	100	100.0
Mar. 30–Apr. 6	200	210	170	193.3	180	200	240	220	210.0	50	210	130.0
Apr. 23–27	100	10	100	70.0	90		90	90	90.0	20	20	20.0
Mean	41.2	32.7	68.3	47.4	42.5	48.9	69.1	39.5	50.0	24.4	39.4	31.9

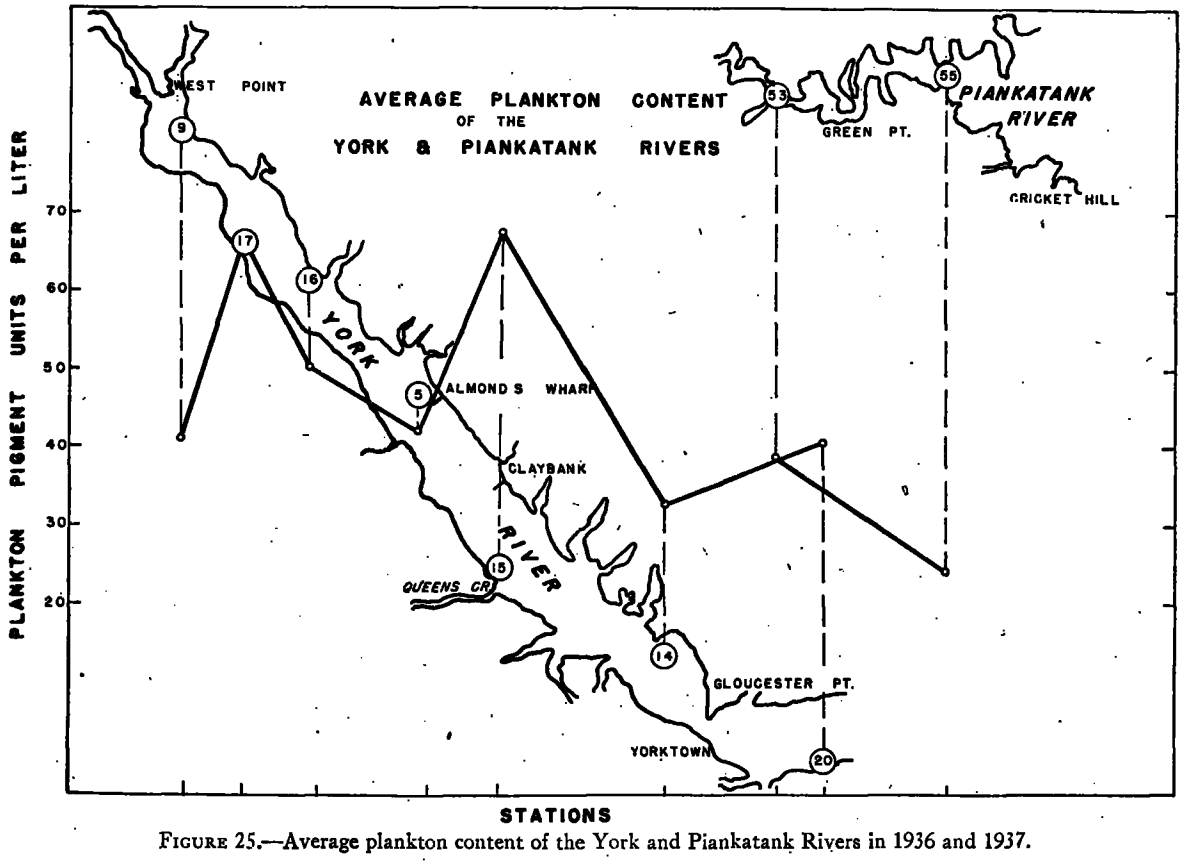

FIGURE 25.—Average plankton content of the York and Piankatank Rivers in 1936 and 1937.

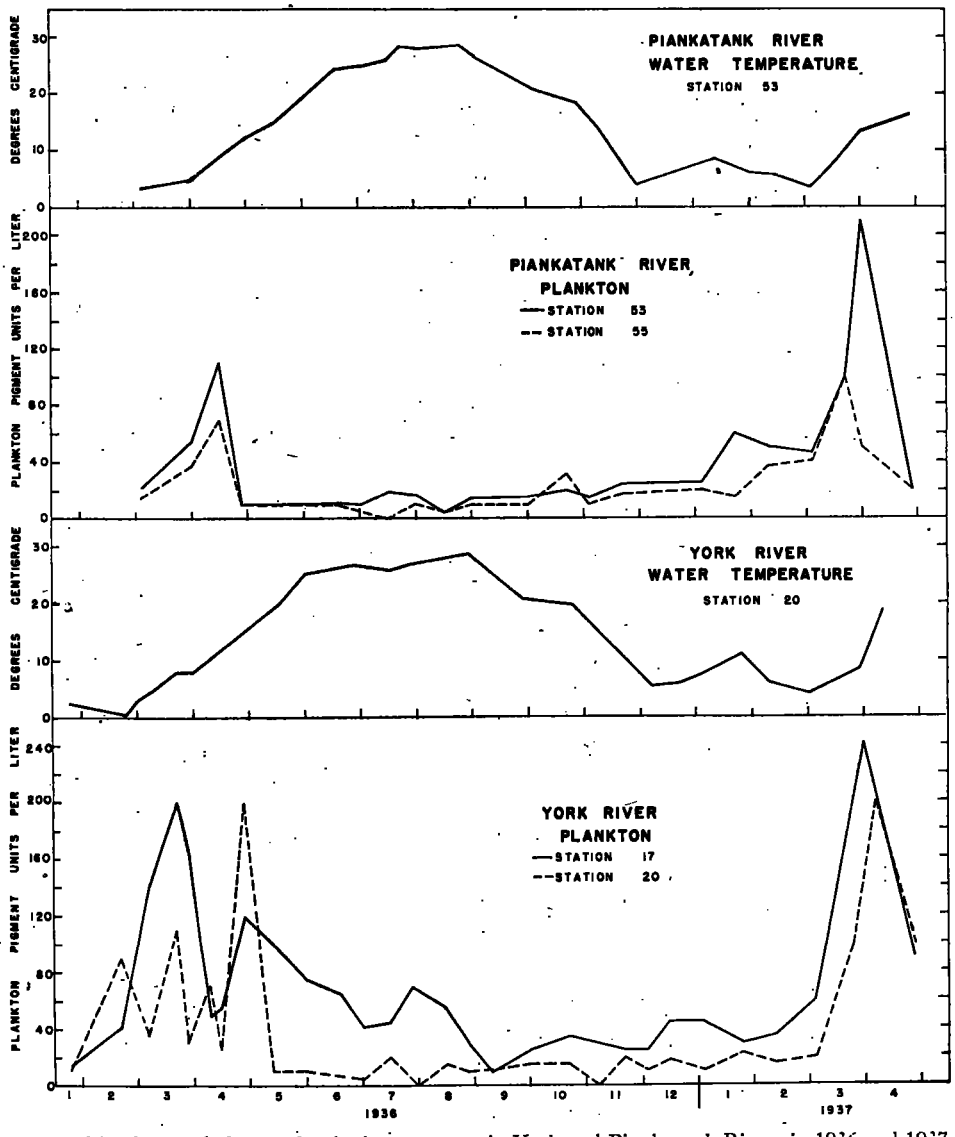

FIGURE 26.—Seasonal changes in plankton content in York and Piankatank Rivers in 1936 and 1937. Pigment-unit method.

Thalassiothrix and *Rhizosolenia* the diatoms listed in the tables are frequently found in the stomachs of the oysters and apparently constitute their normal diet.

The low counts of dinoflagellates may be due in part to the fact that these organisms disintegrate very rapidly in preserved samples (Martin 1923). The plant-pigment method, since it is based on the fresh sample, undoubtedly includes these organisms and in this respect is probably more reliable than the counting of individual forms.

The differences in the number of organisms per liter as determined by plankton counts in the samples from these two stations do not appear to be significant.

Because the nutritive value of various plankton organisms has not yet been determined and we do not know which of them are being utilized by the oyster, the quantitative plankton data gave us no direct reply to the question whether there was an adequate supply of oyster food in York River. It is, however, reasonable to infer that since general productivity of river plankton was not impaired by pollution or other adverse factors, the supply of food needed by the oysters was adequate. Slightly increased plankton production in the upper part of

TABLE 26.—*Number of plankton organisms per liter at station 17 in the York River*

GENERA OF DIATOMS

Date	Nitzschia	Skeletonema	Coscinodiscus	Rhizosolenia	Pleurosigma	Navicula	Thalassiothrix
1935							
Dec. 6	3,900	1,980	984				
1936							
Jan. 7			9,840				
Mar. 6	344,000			9,840	9,840		
Mar. 19	590,000	9,840	39,000			19,800	
Mar. 25	660,000		49,000			39,000	19,700
Apr. 1	560,000		29,500				39,300
Apr. 9	354,000		29,500				
Apr. 16	640,000		118,000			59,000	138,000
June 1			39,000		98,000	39,000	98,000
June 19	78,000					19,680	
July 2	98,000		19,000				39,000
July 17	59,000		39,000		19,000	59,000	98,000
July 1			19,000				78,000
Aug. 17	78,000		39,000			39,000	39,000
Aug. 29	660,000				196,000		39,000
Sept. 10	176,000		54,000		196,000		54,000
Oct. 1			71,000		35,000		
Oct. 22	19,680	19,680			19,680		53,000
Total	4,320,580	31,500	555,824	9,840	573,520	274,480	695,000

TABLE 27.—*Number of plankton organisms per liter at station 20 in the York River*

GENERA OF DIATOMS

Date	Nitzschia	Skeletonema	Coscinodiscus	Rhizosolenia	Pleurosigma	Navicula	Thalassiothrix	Asterionella	Fragilaria	Dinoflagellates
1935										
Dec. 6	7,900	37,000	1,960	984			8,500			
Dec. 23	63,000	5,900	2,900	984	1,970			5,900		
1936										
Feb. 28	440,000		29,000						19,700	
Mar. 4	443,000	78,500		29,000				29,000		
Mar. 30	1,180,000						118,000	264,000		
Apr. 8	265,000			19,800						
Apr. 14	648,000		39,000	59,000						
May 27	118,000		19,000							
June 30										75,000
July 27				12,000	5,800					9,800
Aug. 14			11,800	138,000	1,900					5,900
Aug. 26	3,960			116,000		39,000				3,960
Sept. 14	3,960			5,800		1,968				5,900
Oct. 1	35,400	1,968	1,968							
Oct. 21	13,800			78,400						11,800
Nov. 5	40,600		1,968	31,400			3,960			5,900
Nov. 24	1,968		1,968	1,968						
Total	3,264,588	123,368	109,564	495,304	11,638	40,968	130,460	298,900	19,700	118,260

the river was very likely due to the fertilizing effect of pollutants which contain considerable amounts of carbohydrates and other organic compounds. Laboratory experiments with *Nitzschia* culture described below show that reproduction of this diatom is stimulated by low concentrations of pulp-mill effluent and therefore confirm this conclusion.

EFFECT OF PULP MILL EFFLUENTS ON GROWTH OF NITZSCHIA CULTURE

The effect of pulp-mill effluents on the propagation of diatoms was studied in the laboratory with the use of a marine species, *Nitzschia closterium*, commonly found in estuaries and known to be used by the oyster as food. A vigorous culture of a single species has been maintained in the laboratory for several years without showing any signs of degeneration. The culture was kept in round 150-milliliter pyrex flasks with Miquel solution containing a small amount of sterile soil extract. The flasks were placed in a glass cabinet provided with a temperature control capable of keeping the temperature between 15° and 17° C. Each side of the cabinet was uniformly and continuously illuminated by nine 25-watt Mazda lamps mounted on two adjustable stands and provided with reflectors. Details of the arrangement have been fully described by Galtsoff (1937: 34–35) and need not be repeated here. The densities of *Nitzschia* population in different flasks were determined by means of a Weston photoelectric cell and a sensitive microammeter. In order to convert the readings of

the instrument into the number of cells per milliliter, a calibration table and a curve were prepared by counting the number of *Nitzschia* in various dilutions of stock culture and plotting the results against the readings of the instrument. Intermediate values were obtained through interpolation. Using this technique, which has been already described in previous publications (Galtsoff *et al* 1935), a series of experiments were carried out with the effluent arising from the pulping process (sewers *J* and *H*) added to Miquel solutions in concentrations of 1:1000, 1:10,000. and 1:100,000. In each experiment an equal number of flasks, varying from 2 to 6 were used for the control and for the test. Every day the content of each flask was stirred to avoid settling of the *Nitzschia* on the bottom and the position of the test flask and its control was interchanged to equalize the possible differences in the intensity of illumination. The initial density of *Nitzschia* culture varied between 5,000 and 7,000 cells per milliliter but was always identical in the test flask and its control.

In a first series of experiments, the sample of pulp-mill effluent was sterilized for 15 minutes at 15 pounds pressure. In a second series of tests, raw effluent, stored in the refrigerator, was used.

The growth of *Nitzschia* culture in Miquel solution continues at a definite rate until a maximum population density is reached. After that the slope of the curve gradually flattens and the density of the culture remains more or less constant for many days, or begins to decline probably due to exhaustion of food material and accumulation of metabolites. In testing the effect of pulp-mill effluent, the cultures were usually maintained as long as it was practical, and readings were made at regular intervals. Some of the tests lasted as long as 77 days. During these prolonged tests, the population of *Nitzschia*, after reaching its maximum of about 1,900,000 cells per milliliter, remained constant for at least 2 weeks. It has been noticed that, in several instances, the longevity of cultures kept in the media containing raw pulp-mill effluent was shorter than in the controls or in the flasks with sterile effluent. The degeneration of the cultures was always associated with a sudden increase in bacterial growth, flocculation of *Nitzschia* cells, and their rapid settling on the bottom. In several cases the cultures to which raw effluent was added became badly contaminated with large and fast-moving *Spirillae* and all *Nitzschia* perished. Because of this difficulty, it was impractical to continue the tests with raw effluent for more than 28 days.

Analyses of experimental records clearly show that the addition of effluents in concentrations not exceeding 1:1,000 has no adverse effect on the growth of *Nitzschia* culture. As shown by figure 27, experiment A, the growth in the control culture and in the medium containing sterile effluent is almost identical. The difference is, however, apparent when raw effluent is added in the same concentration (fig. 27, experiment B). Stimulating effect of the effluent also is shown by a more rapid propagation of *Nitzschia*, the difference between the test flasks and their controls becoming more pronounced as the population densities increase.

Table 28 gives a summary of all the tests with sterile (series A) and raw effluent (series B) added in concentrations of 1:1,000, 1:10,000, and 1:100,000. With the exception of one test, B7 (concentration 1:10,000), the final densities of *Nitzschia* cultures grown in flasks with raw effluent were greater than in the controls. This difference was not observed when sterile effluent was used.

Raw effluent added in concentrations of 1:100 inhibits the growth of *Nitzschia*, as can be clearly seen from table 29, which summarizes these tests.

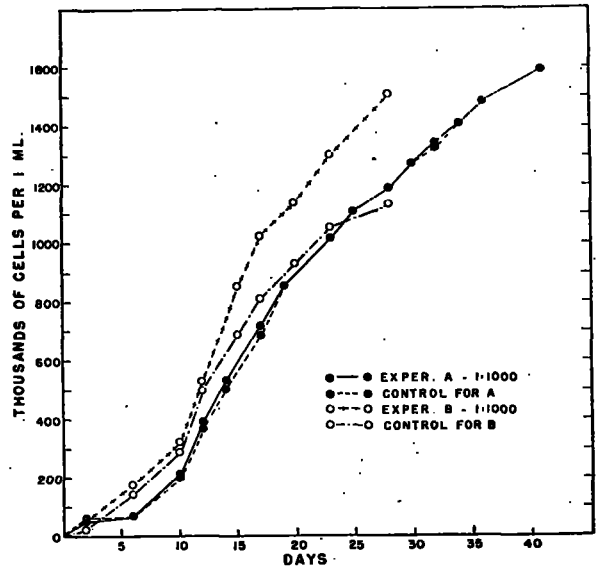

FIGURE 27.—Growth of *Nitzschia* culture in Miquel solution containing sterile and raw pulp-mill effluent in the concentration of 1:1,000. Experiment A (solid circles), sterile effluent; experiment B (open circles), raw effluent. Temperature 15°–17° C.

Concentrations less than 1:100,000 have little or no stimulation as compared with the controls.

The laboratory experiments demonstrate that low concentrations of pulp-mill waste stimulate the growth of *Nitzschia* culture. They are in accord with the field observations, which disclosed greater abundance of phytoplankton in the upper York River, polluted with pulp-mill effluents, than in its lower part where pollution is not noticeable.

TABLE 28.—*Densities of Nitzschia cultures at the end of tests in Miquel solution (control) and in various concentrations of pulp-mill effluent*

[Tests A1 to A13 made with sterile effluent; tests B1 to B12, with raw effluent. In all tests, figures given in the table represent the densities of populations before they began to decline]

Experiment No.	Concentration of effluent	Days of growth	Thousands of *Nitzschia* in 1 milliliter	
			Sterile effluent	Control
A1	1:1,000	40	1,370	1,750
A2	1:1,000	40	1,275	1,610
A3	1:1,000	60	1,600	1,775
A4	1:1,000	60	1,600	1,775
A5	1:1,000	77	1,300	1,900
A6	1:10,000	60	1,755	1,740
A7	1:10,000	60	1,755	1,740
A8	1:10,000	77	953	1,800
A9	1:10,000	77	1,900	1,900
A10	1:100,000	77	1,750	1,755
A11	1:100,000	77	1,710	1,800
A12	1:100,000	77	1,900	1,330
A13	1:100,000	77	1,610	1,183

Experiment No.	Concentration of effluent	Days of growth	Thousands of *Nitzschia* in 1 milliliter	
			Raw effluent	Control
B1	1:1,000	25	1,750	1,175
B2	1:1,000	25	1,150	825
B3	1:1,000	25	1,235	1,090
B4	1:1,000	14	1,100	675
B5	1:1,000	14	1,075	680
B6	1:1,000	14	1,035	805
B7	1:10,000	22	1,075	1,225
B8	1:10,000	22	955	900
B9	1:10,000	25	1,115	955
B10	1:100,000	21	1,300	1,025
B11	1:100,000	21	1,230	1,025
B12	1:100,000	16	1,025	775

TABLE 29.—*Inhibition of Nitzschia growth in strong concentration of raw pulp-mill effluent*

[The concentration used was 1:100 and the period of growth was 20 days]

Experiment	Thousands of *Nitzschia* in 1 milliliter	
	Effluent	Control
1	425	891
2	442	1,028
3	435	998
4	416	1,013
5	404	998
6	396	1,013

CONDITION OF THE OYSTERS OF THE YORK AND PIANKATANK RIVERS

The condition of the oysters in the York River was carefully followed throughout the time of investigation. There were, of course, fluctuations in the condition of all the oysters at the different seasons of the year and in different years. Determinations of the glycogen content and of the percentage of water in the meat confirmed the general impression, gained by inspection, that, regardless of the season, the oysters of the York River above Claybank were poor, while those below it and in the Piankatank River were generally good. The oysters on the right shore of the York River were usually in better condition than those on the left shore, and in some respects the oysters in the vicinity of Bell Rock and above were a little better than those just below. The poorest oysters were found on the grounds from just below Bell Rock Lighthouse to a point just above Claybank Wharf, and particularly on grounds off Poropotank and Purtan Bays.

The meats of the poor oysters were found to be watery and emaciated, with brownish or greenish discoloration of the mantle, gills, and labial palps. The shells of these oysters were very thin and fragile and often contained mud vesicles. Aside from the poor quality of the meat, the shell condition was a factor that made the oysters of this area unmarketable, or marketed with great difficulty. In many instances there was a failure of gonad development.

SHELLS OF THE YORK RIVER OYSTERS

The majority of oysters from the upper part of the York River had thin, fragile shells. In various degrees of intensity this condition prevailed among the oysters grown above Claybank, and was especially pronounced in the specimens taken at stations 9 (at Goff Point), 22 (Purtan Bay), and 23 (between Allmondsville and Claybank). Similar conditions were observed in the oysters brought by J. E. Scanlon and other oyster growers to the shellfish laboratory in Washington in the spring of 1934, before the initiation of the present investigation.

Adult York River oysters varied from 3½ to 4¾ inches in length and from 1¼ to 3½ inches in width. Long and narrow oysters were more abundant in the upper part of the river, whereas wide and rounded specimens predominated in its lower part (fig. 29).

So thin were the shells of many specimens obtained from the upper part of the York River that the valves, when examined in a transmitted light, were transparent. The shells of these oysters were so fragile that they crumbled under a slight pressure of a finger. Cases of infestations by mudworms (*Polydora*) and boring sponge were frequent. In several instances, the shells of live oysters were almost completely destroyed by the boring sponge. There were, however, many specimens that were entirely free from infestation, yet had extraordinarily fragile and thin shells. This abnormal condition of the shells suggested either a deficiency of calcium in the sea water or some morbid state of the organism, which might have resulted from a functional disturbance or an infectional disease interfering with the calcium metabolism.

The first possibility was explored by determining the amount of calcium in the sea water. It was considered possible that sulfates and lignin, found in considerable quantities in the pulp-mill effluent discharged at the head of the river, had a tendency to precipitate calcium carbonates and upset the ionic equilibrium of sea water. If this were the case, the analyses of samples of sea water collected from the upper and lower parts of York River would have revealed the relative degree of Ca depletion. Determinations made according to the method of Meloche and Setterquist (1933) gave the following results:

Station	Calcium Milligrams per liter	Chlorine Milligrams per liter	$\frac{Ca}{Cl}$
16 (upper part)	102.1	4,610	0.02215
14 (lower part)	204.0	8,630	.02363

The difference in the concentration of Ca in the two sets of samples depends, of course, on the salinity of water, but the ratio of Ca:Cl does not show a significant difference between the upper and lower parts of the river. The values of Ca:Cl ratios, representing the averages of four samples, are slightly greater than the Ca:Cl ratios calculated from the data available for various parts of the ocean. The latter vary from 0.02112 to 0.02266 (Th. G. Thompson and R. J. Robinson 1932:119), the "best" value according to Lyman and Fleming (1940) being 0.02106. Since the calcium-chlorinity ratio in the York River did not significantly differ from the values usually encountered under normal conditions, further observations along this line were discontinued.

There was no evidence that defects in the calcification of shells of York River oysters could be correlated with the disturbance of the calcium equilibrium in the water; it is reasonable to suspect that they were due to the functional failure of the lime-depositing organs.

Shape, Area, and Weight of Shells

Field examinations of a large number of samples from the upper part of the river indicated that the poorest oysters were invariably those with long, narrow, and very thin shells (fig. 29). It was therefore of interest to compare the areas and weights of shells of the oysters from the polluted area with those from the lower part of the river and from the adjacent areas which are free from pollution. Obviously, such a comparison should be made between oysters of the same age that grow for the same length of time in the river. This, however, presented considerable difficulty because of the changes in the oyster populations on various grounds caused by oyster-farming operations. During the time of observations, and in the preceding years, oystermen were transplanting their stock from one ground to another and occasionally were bringing in oysters from the outside. Fortunately, there were several areas of abandoned bottoms which still contained fairly large numbers of oysters. By making a thorough inquiry, the authors were able to avoid the bottoms that were recently planted and take samples from the areas which contained only so-called native oysters. The latter term is used here only for the sake of convenience and denotes oysters

FIGURE 28.—Cross section of the left shell of an oyster from the upper part of York River. The section is made at the level of the muscle scar; the cloacal side is on the left. Notice the large cavities either empty or filled with loose chalky deposit; magnified 3½ times.

which remained in the York River not less than four years. Undoubtedly, some oysters grew from local set, but the majority were planted as seed from the James River. On October 11 and 12, 1938, samples of these oysters were collected from eight stations in the upper part of the York River above Claybank. Three weeks later, on October 31, samples were obtained at five stations distributed in the lower part of the York River, in its mouth, and in the Piankatank River. Oysters comprising the second group were taken from waters not affected by pulp-mill pollution and appeared to be in every respect normal. Unfortunately, the exact age of these oysters could not be ascertained. Examination of planting records of local oystermen convinced us, however, that oysters collected from various stations in the lower part of the York River and vicinity were at least 5 years old. Oysters from the upper part of the river, where planting operations ceased long ago, were probably not less than 6 or 7 years old.

The purpose of our comparison was to determine whether there was a significant difference in the weight of the shells in oysters from different stations which may have suggested that the deposition of calcium carbonate and growth of shell was affected by local conditions. Unfortunately, a number of specimens obtained at various stations had to be rejected because their shells were riddled by the boring sponge and the determination of their weight would have been misleading. This so reduced the number of oysters available for measurements that no more than eight specimens could be accepted from each station. The comparison has to be made, therefore, only between the two larger groups of shells, one from the upper York River (group B) and one from the lower York and Piankatank Rivers (group A). After removing the encrusting organisms and dirt, the shells were dried at 60° C. for 24 hours and both valves of each oyster weighed to the nearest decigram. The area of the shell then was determined by placing the left valve, which is usually the largest, on a sheet of thin paper and obtaining its contour and measuring the area with a planimeter. The results were expressed as total areas, in square inches, and as a weight of both valves per square inch of shell area. Fortunately, oysters of this section have rather flat shells without the pronounced ridges which sometimes are conspicuous in the shells from other sections of the coast. Consequently, it has been assumed that an error due to the unevenness of the shell surface was insignificant.

There appears to be no significant difference in the areas of shells in the two groups of oysters, the means for groups A and B being 7.38 ± 1.68 and 7.64 ± 2.28, respectively.

The test of significance and the necessary statistics given in table 30 show that the "t" value is 0.722 and the difference between the two means is, therefore, entirely within the probability of random sampling.

TABLE 30.—*Comparison of the means of surface areas of shells of oysters from the upper York River (B), and the lower York River and the Piankatank River (A)*

Group	Number of shells	Degrees of freedom	Mean of surface area	Sum of squares
			Square inches	
A	49	48	7.38 ± 1.68	159.816
B	60	59	7.64 ± 1.28	235.980
Difference			0.26	
Total		107		395.796

The weight of shell per square inch of area is significantly higher in the oysters from the unpolluted section (group A) than in those from the polluted area of the York River (group B), the means being 13.43 ± 0.50 and 10.40 ± 0.28, respectively. The test of significance (table 31) gives the value of $t = 5.63$ showing that the difference far exceeds the probability of random sampling.

TABLE 31.—*Comparison of the means of weight of shells per square inch of oysters of the upper York River (B) and the lower York River and the Piankatank River (A)*

Group	Number shells	Degrees of freedom	Mean weight per square inch	Sum of squares
			Grams	
A	49	48	13.43 ± 0.50	594.369
B	60	59	10.40 ± 0.28	271.317
Difference			3.03	
Total		107		865.686

From the analyses of areas and weights of shells, an inference can be made that, with respect to the mean area of shells, the two groups of oysters do not differ from each other, although they can be easily distinguished by their shape. As to the weight of shells, oysters from the upper part of York River are unquestionably lighter than those from its lower part and from the Piankatank River. It is natural to suppose that the difference is brought about by a slower rate of calcium deposition in these oysters. Light weight of oyster shells from the upper part of the York River is due to their thinness, and to the presence of large cavities filled with loose chalky material instead of more compact, and therefore

heavier, layers of crystalline calcium carbonate. Very often adult oysters were found in which the thickness of the shell varied from 0.5 to 1.50 millimeters. The prevailing thickness of shell in the oysters of the lower part of the river was usually from 4 to 10 millimeters. As oyster shell is not of uniform thickness, considerable difference always can be noticed in the same valve. However, no oysters with thin, transparent shells were found except in the upper part of the York River.

It also has been observed that the central parts of the shells of group-B oysters (upper York River) were the thinnest, and that the thickest portion of the shells, was at the edge. This is readily seen in figure 28 representing the cross-section of the right valve of an oyster from station 5. It seems that the deposition of shell material along the central part of the valve was inhibited. The tendency to deposit more shell material at the edges than at the central portion of the valve frequently can be found in oysters from Long Island Sound, Louisiana, and Texas. Some of the very heavy shells, more than 1-inch thick, collected by Galtsoff in Louisiana, showed increased thickness at the edges. In some of these specimens the thickening was restricted to the left valve only, while in others it was pronounced on both sides of the body. It is therefore probable that irregularity in the deposition of shell material frequently occurs in oysters and attracts no attention if the valves remain fairly thick. So little is known, however, about the physiology of shell formation in the oyster and other lamellibranchs that interpretation of these observations must wait until the underlying biological processes are better understood.

Presumably, the shell material of the oyster acts as a buffer. Part of it dissolves in the shell liquor when the valves are closed and through the accumulation of CO_2 the acidity of the liquor increases and the inside of the shell is corroded. Dugal and Irving (1937) have demonstrated this for the clam, *Venus*. Marks of etching on the nacreous layer are easily noticeable in the clam but cannot be observed on the oyster shell deprived of true nacre. The possibility that in the oyster a certain portion of the inorganic part of the shell material may be lost through dissolution in the shell liquor does, however, exist. The dissolution of salts may become more pronounced the longer the mollusk remains closed. Whether this condition is responsible for the thinness of the York River shells has not been ascertained, for the evidence of such an occurrence is rather difficult, if not impossible, to obtain. Yet it appears desirable to indicate this possibility, for it will be shown later that the presence of pulp-mill pollutant increases the duration of closure of shells in York River oysters.

PATHOLOGICAL STUDIES

Structure of Shell

In view of the pronounced abnormality in the consistency and thickness of shells of many oysters taken from the upper part of the York River, it was considered desirable to study the shells in a more detailed manner and to determine whether the microscopic structure of these shells would reveal any pathological condition. Thin transverse sections of shells were made by grinding small pieces that were mounted on glass slides with heated Bakelite varnish. For grinding to the desired thickness, a motor-driven silicon-carbide resinoid wheel was used. After grinding, the preparation was air-dried and mounted in Canada balsam.[5] The presence of large pockets of chalky material presented considerable difficulty, and many preparations were lost before the grinding was completed. Several satisfactory preparations, however, were made and used for comparison with the normal-shell structure.

The literature on the composition and structure of mollusk shells comprises many papers written by zoologists, mineralogists, and chemists. Because of the different points of view from which shell studies were made, it is difficult to correlate the microscopic structure of shell with its crystallographic characteristic and with its chemical composition. A review of the extensive literature, scattered in zoological, mineralogical, and geological publications, and which frequently contained contradictory statements, is not necessary for the present discussion. It suffices to mention that in accordance with the present views, lamellibranch shell consists of three layers: (*a*) an outer layer of horny substance, conchyolin, secreted by the epithelium of the groove at the free edge of the mantle; (*b*) an underlying prismatic layer, also formed at the edge of the mantle; and (*c*) an internal nacreous layer which is secreted by the epithelial covering of the body and mantle. The described arrangement is typical for fresh-water Unionidae and marine Aviculidae and Mytilidae. In other lamellibranchs it occurs with certain modifications. In

[5] For the details of the technique and suggestions regarding the necessary equipment, the authors are grateful to Dr. L. G. Henbest of the U. S. National Museum who perfected this method.

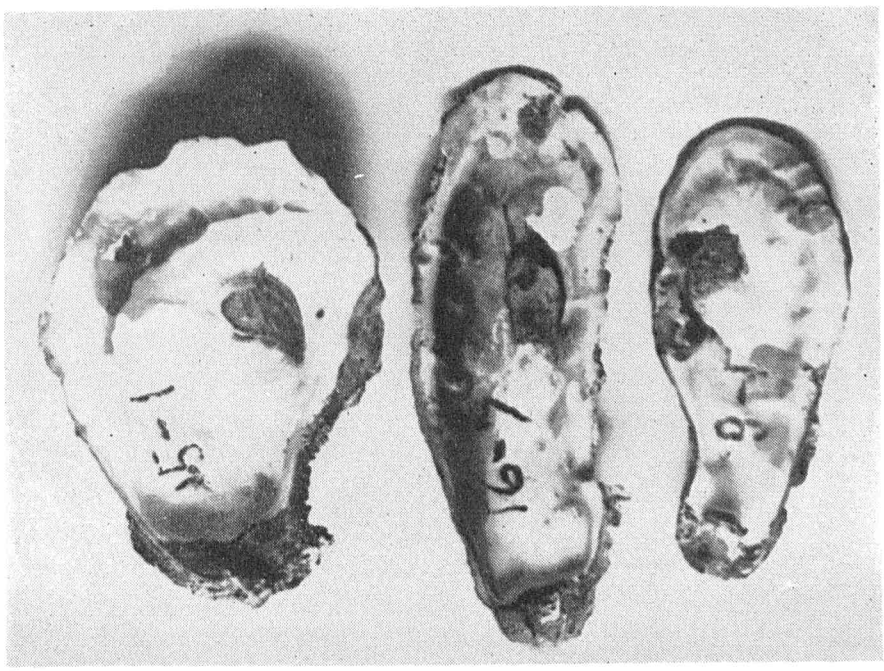

FIGURE 29.—Shells of adult York River oysters. The two shells on the right are from the upper part, and the shell on the left is from lower part of the river.

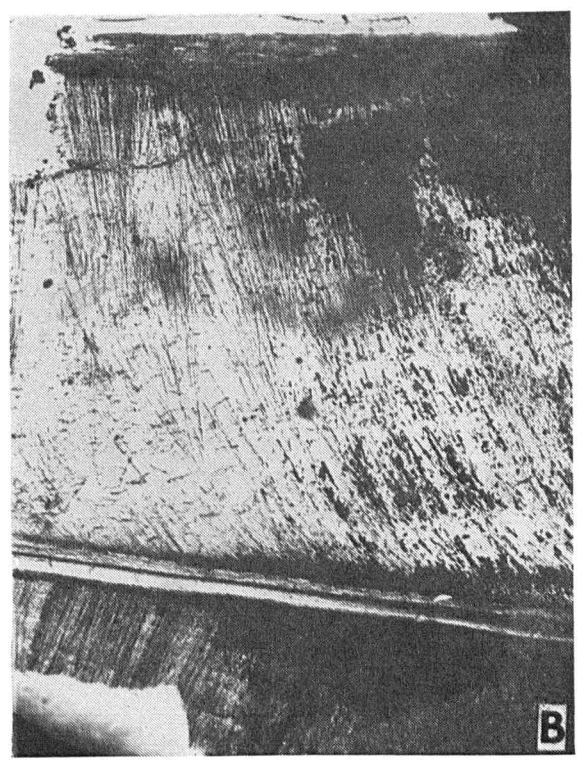

FIGURE 30.—Photomicrograph of horizontal (*A*) and vertical (*B*) sections of the shell of a York River oyster. *A*, × 80; *B*, × 50. Notice the radial arrangement of structural elements in *A*. Dark spots in the upper part of *B* are the deposits of chalky material. Horizontal layer in the lower part is a series of compact lamellae.

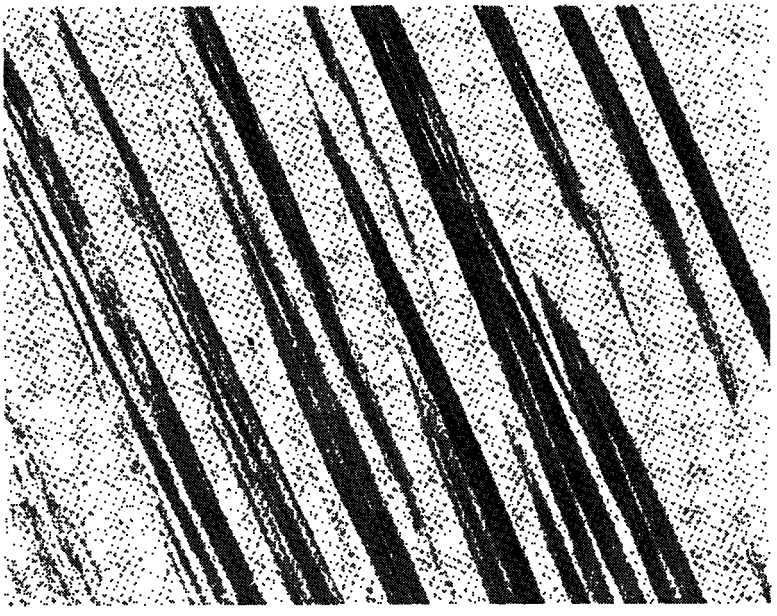

FIGURE 31.—Photomicrograph of the adductor muscle fixed in relaxed state. Iron haematoxylin-eosin. Vertical section. Note slightly swollen dark areas. × 250.

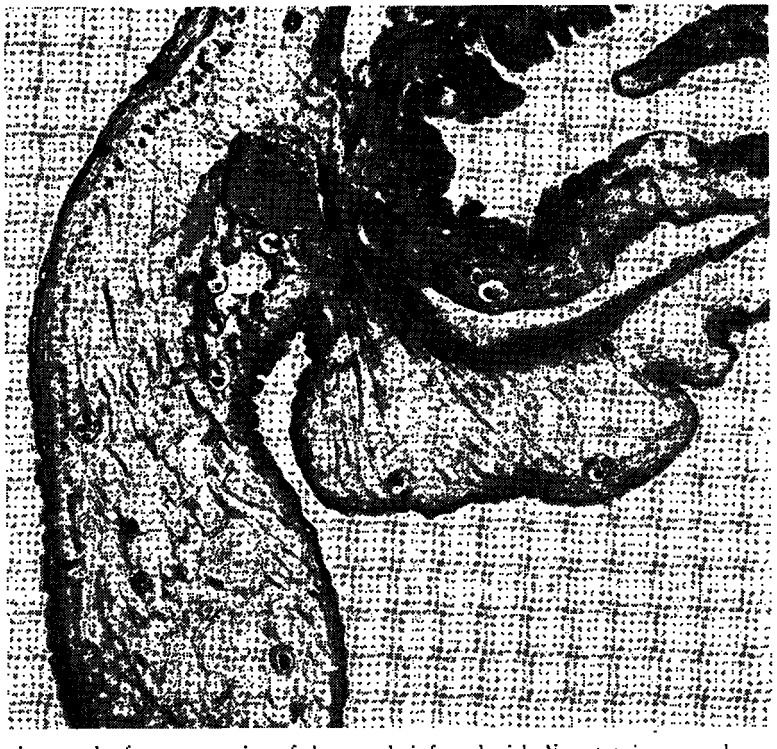

FIGURE 32.—Photomicrograph of a cross section of the mantle infected with *Nematopsis* spores; haematoxylin-eosin. × 125.

Ostrea the outer horny layer (periostracum, or epidermis of many authors) is not well developed and its existence is doubted by some of the investigators. In our preparations a very thin homogeneous layer, not impregnated with calcium salts, can be seen over the prismatic layer of the shell. It is, however, very poorly developed.

The prismatic layer, as the name implies, consists of regular and distinct prisms of calcified material embedded in conchyolin substance and oriented normally to the surface of the shell. It often can be found as a scale-line formation on the exterior of the shell and at its edges. This layer is rather thin and often absent in old shells.

The inner layer of the shell consists of a substance different from the true nacre of other lamellibranchs, and is characterized by a very irregular arrangement of structural elements, oriented horizontally, obliquely, and sometimes even vertically (at right angle to the surface of shell). In preparations ground parallel to the surface of the shell, this layer is seen to consist of large alveoli with vertical laminae radiating from their centers (fig. 30A).

Typical for the genus *Ostrea* (Böggild 1930) is the fact that the layers of normal consistency may alternate with more or less loosely packed layers of chalky substance, placed vertically, and oriented at all possible angles around the normal (at right angle to surface) axis of the shell (fig. 30B). The chalky deposits (called in French *chambrage*, chambering) were investigated by Orton and Amirthalingam (1927), who advance a theory that they are caused by the shrinkage of the body after spawning or when the oyster is transferred from high to low salinity. Subsequent automatic secretion of material by the surface of the shrunken body, destined normally for thickening of the shell, seals the liquid which percolates between the oyster's body and the shell and forms a chamber. Further deposition of the nacreous layer serves to conceal the chamber permanently. If we accept this explanation, which requires further corroboration, an inference must be made that chalky material is precipitated from the liquid sealed in the chamber and is not secreted by the mantle epithelium. More detailed observations are necessary to settle this interesting point. Chambering has also been observed in *Ostrea* (*Gryphaea*) *angulata* and in several fossil forms such as *Gryphaea vesicularis*, *Ostrea hippopodium*, and *Ostrea reflexa*. Presence of large cavities filled with calcite crystals are typical for the shells of these species. These facts lead us to infer that chambering is a normal tendency in various species of oysters. There is no reason, therefore, to regard it as a symptom of pathological conditions.

Examination of preparations made from fragile and thin shells of York River oysters discloses the presence of the same structural elements as are found in normal shells. The only noticeable difference is in the thickness of the shell, not in its component parts. We conclude from these observations that the functioning of shell-secreting organs was proceeding normally except that the rate of deposition of calcium salts was reduced, probably by environmental conditions. The experience of local oystermen, who claim that oysters transplanted from the upper part of the river to its mouth or to Mobjack Bay resume good growth and develop stronger shells, corroborates this inference.

Microscopic Examination of the Tissues

Oysters of poorest quality, i. e., watery with emaciated and discolored tissues and thin transparent shells, were selected and preserved in Bouin III, Fleming, and 10 percent formalin solutions. Some of the material, after a brief immersion in 10 percent formalin, was sectioned by using the freezing-microtome technique and stained with Sudan III, IV, and haematoxylin. Other specimens were embedded in paraffin and stained with Heidenhain iron haematoxylin, Delafield haematoxylin, and counterstained with eosin, safranin, and mallory. All the organs, namely the mantle, gills, heart, digestive gland, intestine, gonads, adductor muscle, viscera, ganglia, and circumpallial nerve, were examined. These studies revealed no pathological conditions in these organs with the exception of the occasional occurrence of abnormal fibers in the adductor muscle. Both in smooth and striated portions of the muscle, fibers were found which were abnormally swollen, and in some instances surrounded by very thin capsules. Although the homogeneous and transparent substance of the fiber had no increased affinity for eosin, it somewhat resembled the first stages of hyaline degeneration found in mammalian tissues (Vines 1934: 210). In the latter cases the degenerated mass is usually eosinophilic. The affected muscle fibers of the oyster had, however, strong affinity for iron haematoxylin and retained black color in the preparations in which other parts of the muscle remained almost completely unstained (fig. 31). This condition has been observed

by Prytherch (1940) in the muscles of oysters infected by *Nematopsis*. In our preparations, abnormal muscle fibers were found both in the infected and non-infected specimens. Muscular degeneration in weak, European oysters (so-called "hockley" oysters) was described by Orton (1924), who found microscopic spindle-shaped bodies throughout the tissues remote from the adductor muscle. His experiments with healthy oysters, the shells of which were bored and the adductor muscles pierced, showed that the spindles could be produced artificially. He thinks that these spindles may arise from the degeneration of the muscles of the mantle. No spindles answering Orton's description were found in the York River oysters. The abnormal fibers of York River oysters were much longer and wider than those described by Orton and were found only in the adductor muscle. So little is known about the muscular degeneration in mollusks, and in lamellibranchs in particular, that no interpretation of the observed condition is at present possible.

Careful examination of other tissues, i. e., mantle, gills, labial palps, digestive gland, nervous ganglia, intestines, heart, and excretory organs, revealed no pathological or degenerative conditions. The connective tissue of the body wall and mantle contained large numbers of pigment granules insoluble in alcohol and xylol, but similar granules, although in smaller number, occur in other oysters. In the preparations fixed with osmic acid, large black globules were abundant in the mantle and in the body wall, occupying almost the entire space inside the vesicular cells. Sections of fresh material, made with the freezing microtome and stained with Sudan III and IV, proved without any doubt the fatty nature of the globules. No traces of these globules could be found in the preparation treated with ethyl alcohol or other fat solvents. Similar globules were found in healthy oysters from Onset, Mass., Milford, Conn., and Beaufort, S. C. Apparently infiltration of connective tissue with fat is a normal phenomenon not noticeable in the preparation dehydrated with alcohol.

Infection with Nematopsis Spores

In the course of the histological examination, it was noticed that many specimens were infected with spores of a gregarine *Nematopsis*. This microorganism was first described by European protozoologists (Schneider, 1892, Leger and Duboscq, 1903, 1913; and Hatt, 1931) who found it in various lamellibranchs, such as *Cardium*, *Mytilus*, *Anomia*, *Tapes*, *Solen*, and *Ostrea*. In the United States the spores of *Nematopsis* were first reported in 1930 by Prytherch (1940) in the oysters of Mobjack Bay, Va., and later recorded by him from North Carolina and Louisiana. The life cycle of this protozoan was described by Kudo (1939) and Prytherch (1940). Since the initiation of the York River investigations, the distribution of *Nematopsis* in the lower Chesapeake Bay and adjacent waters was studied by Galtsoff and Engle, who were able to extend their observations to other coastal States including Connecticut, New York, Delaware, Alabama, and Texas. In 1941 Galtsoff (unpublished report, Fish and Wildlife Service) found that Texas oysters from Aransas Pass, Mesquite Bay, Karankawa Reef, Lap Reef, Jordan's Pass, and Borup Reef were heavily infected with *Nematopsis* spores. In some instances, oyster tissues contained countless numbers of cysts, especially in the mantle, gills, and in the heart. There was no unusual mortality among the infected oysters and the appearance of their bodies varied from fair to good. Only in cases of extremely heavy infection were oyster meats poor. In 1941 the Louisiana Department of Conservation (unpublished data collected by Gowanloch and Kavanaugh) reported that *Nematopsis* was present on nearly all oyster grounds within the State's waters, in many instances, infecting all the oysters on the reef. The State investigators were unable to find any correlation between the intensity of *Nematopsis* infection and the mortality which occurred at that time on some of the grounds.

Oysters heavily infected by *Nematopsis* were collected in 1943 by Engle (1945) in Mobile Bay in the area of Dauphin Island (Mississippi Sound). The infection was so heavy that the gills of the specimen examined by Galtsoff appeared to be full of cysts which could be easily washed off by shaking the tissues in water. Although these oysters were in poor condition, they were not dying, and no reports were received later of any noticeable mortality among them.

In 1942–43 Galtsoff found that oysters on public seed-grounds and on planted bottoms in the Delaware Bay were infected with *Nematopsis* cysts. Since it was known that during the preceding year some of the infested seed oysters were shipped to Connecticut and New York for planting in Great South Bay and in Long Island Sound, attempts were made to locate them. Some of the oysters grown from this

seed were collected for examination and found lightly infected. Planters reported no unusual mortality among this stock which grew and fattened in a normal way.

The range of distribution of *Nematopsis*, as shown by these observations, extends from Texas to Delaware Bay with occasional infection of oysters in Great South Bay and Long Island Sound. So far *Nematopsis* has not been found in waters of Rhode Island, Massachusetts, New Hampshire, or on the Pacific coast.

Infection with this microorganism can naturally be suspected as one of the possible causes of the pathological condition of York River oysters. An answer to this question is given by the results of a systematic examination of oysters collected at various sections of the river. At each sampling station, 20 oysters were obtained for microscopic examination of their organs and tissues. Each specimen was dissected and preparations were made of the mantle, gills, labial palps, heart, and both parts of the adductor muscle. The highest infection was found to occur in the mantle.

Examination of 200 oysters collected at various times during the year of 1936 at 10 different stations between West point and Yorktown shows that 86 specimens, or 43 percent of them, were not infected. In this examination the following technique was used: a piece of tissue or organ, about 1 centimeter square, was cut from the body and placed between two slides which were strongly pressed together and held in that position with a pair of self-closed forceps. Very strong illumination and a magnification of 250 were employed. By using a mechanical stage, the entire slide, representing 1 square centimeter of the original section of the tissue, was examined and the total number of cysts found in it recorded. No counts were made when the number of cysts exceeded 200 per field. In several cases of very heavy infection of the mantle, the number of cysts per square centimeter was estimated to exceed 5,000. In other organs it varied from 0 to 30. In order of the frequency of infection, the organs can be listed as follows: mantle, adductor muscle, heart, labial palps, and gills. No cysts were found in the digestive gland, gonads, and excretory organ. A summary of these examinations is given in table 32.

In 29 percent of those with infection of the mantle, the number of cysts was very great, exceeding 200 per square centimeter. Next in the frequency of infection was the adductor muscle (41.2 percent), in which the number of cysts was always small. The gills were found to be infected only in 10.5 percent of parasitized oysters. This low percentage is rather surprising, for one may have expected that the organs engaged in the pumping of water in which the gymnospores of *Nematopsis* are suspended would have a greater opportunity to be invaded by the micro-organism.

TABLE 32.—*Frequency of occurrence of* Nematopsis *in various organs of 114 infected oysters from York River*

Infected organs	Number of oysters in which infection was found	Percentage
Mantle	69	60.5
Adductor muscle	47	41.2
Heart	29	25.4
Labial palps	15	13.2
Gills	12	10.5
Digestive gland	0	0
Gonads	0	0

The infection with *Nematopsis* can naturally be suspected as one of the possible causes of the poor condition of York River oysters. An attempt to answer this question was made by recording the condition of oysters examined for the presence of *Nematopsis* spores. The results of the observations are summarized in table 33, which shows the date of collection, the distance of the station from West Point, condition of the oysters, percentage of infected specimens in the sample, and intensity of infection. The latter is expressed in the following arbitrary terms: heavy—widespread infection, number of cysts in the mantle exceeding 1,000 per square centimeter; medium—cysts in two or three organs, number of cysts in mantle less than 1,000 per square centimeter; light—occasional cysts in one or two organs.

TABLE 33.—*Infection of York River oysters with* Nematopsis

[20 oysters were examined at each station]

Station No.	Approximate distance from West Point	Date	Condition	Percentage infected	Intensity of infection
	Miles	*1936*			
9	2.0	July 31	Poor	88	Heavy.
8	4.5	Aug. 17	Very poor	56	Medium.
17	5.5	June 19	Poor	71	Light.
16	6.5	Aug. 5	do	16	Do.
6	8.5	Nov. 10	Very poor	12	Do.
22	10.5	July 16	Poor	96	Do.
22	10.5	Nov. 24	do	56	Do.
		1937			
22	10.5	July 6	do	100	Heavy.
		1936			
15	16.5	Aug. 27	Good	87	Medium.
14	23.0	July 27	do	48	Light.
20	29.0	June 2	do	0	

If the infection of oysters with *Nematopsis* is the primary cause of their poor condition, one should expect the poorest oysters to be those the most heavily infected. Observations, however, do not support this conclusion. The poorest oysters of the entire section, found at station 6 (table 33), showed a rather low percentage of infection, and those found in fairly good condition (station 15) were more heavily infected. Furthermore, a decrease in the percentage of infected oysters from 96 to 56, as observed at station 22, was not accompanied by any noticeable improvement in their quality. Convincing evidence that the primary source of trouble is not a parasitic infection was the observation that the condition of the meats of the heavily infected oysters from stations 6 and 22 was not worse than the condition of the meats of the noninfected specimens collected at the same time from the same stations. This observation eliminates *Nematopsis* as a factor responsible for the poor quality of the York River oysters and indicates that their pathological condition is due to some other cause. This inference is further corroborated by the fact that spores found in tissues are inactive, i. e., they do not propagate within the body of the oyster.

Microscopic examination of infected tissues (fig. 32) reveals no inflammatory or other pathological processes in the infected organs. The mesenchyme tissue of the mantle and the pallial nerve in the immediate vicinity of the encapsuled cysts were normal. Likewise, no pathological conditions were observed in the adductor muscle infected with cysts. As stated, abnormal muscle fibers were found both in the infected and noninfected muscles and therefore the condition could not be attributed to the presence of the parasite. It would be reasonable to expect some pathological reaction if the tissue were suffering from the presence of spores. From the microscopic study one may conclude that the encapsuled spores do not affect the host organism, except possibly in extreme cases, such as encountered by the authors in only two Alabama oysters, where the water tubes and passages of the gills were clogged with millions of spores. Even in this case there was no mortality among infected oysters.

METAL CONTENT OF THE YORK RIVER OYSTERS

The presence of blue or greenish discoloration in the tissues of oysters suggests the accumulation of an excess of copper. In order to determine this, analyses were made during the summer of 1937 of copper, iron, manganese, and zinc content of oysters collected at station 22 in the upper part and station 14 in the lower part of the York River. In preparing the samples for analyses, the following procedure was followed; one to two grams of the dried sample were weighed into a silica crucible, charred over a low flame, and then ashed in the muffle at a temperature of 500° C. for 3 to 4 hours. The sample was cooled, and moistened with water. Then 1 milliliter of concentrated HNO_3 was added, and the sample evaporated to dryness on the hot plate and returned to the muffle for one hour at a temperature of 400° C. Ashing was usually completed after one application of HNO_3. The cooled ash was dissolved in 15 milliliters of 1:1 HCl. Then 10 drops of 30 percent H_2O_2 were added to the solution, which was then heated until the oxygen ceased to be liberated. The sample was then transferred to a 100-milliliter volumetric flask and diluted to the mark. The water used in solutions and reagents was redistilled in pyrex containers and was frequently tested for copper and iron and found to be free from traces of these metals.

Copper was determined as a thiocyanide-pyridine compound using Biazzo method with modifications described by Elvehjem and Lindow (1929) and Elvehjem and Hart (1931). Kennedy's thiocyanate method (1927) was used for Fe determination. Manganese was determined by the periodate method of Willard and Greathouse, modified by Richards (1930). All colorimetric determinations were made by comparing the unknown with standards in a Duboscq colorimeter. Zinc was determined as potassium zinc ferrocyanide using a Duboscq nephelometer for turbidimetric estimation (Birckner 1919).

The results of the analyses (table 34), expressed in milligrams of metal per kilogram of dry meat, show considerably higher content of all four metals in the oysters of the upper part of the river than those taken from its lower section. The last three lines of the table are introduced for comparison to show the metal content of the three samples of oysters collected

TABLE 34.—*Metal content of York River and Norfolk oysters in milligrams per kilo, dry basis*

Source	Date	Iron	Copper	Manganese	Zinc
Station 22	July 23, 1937	1,210	782	59.9	9,240
Station 14	do	452	326	25.7	6,120
Near Norfolk	October 1931	495	299	19.5	------
Do	do	322	164.3	14.9	------
Do	do	1,040	135.6	22.4	------

in October 1931 in the vicinity of Norfolk and analyzed by E. J. Coulson.

In general, there is no significant difference in the metal content of the York River oyster and those from the vicinity of Norfolk. (The latter samples were taken from commercial plantings and their exact origin is not known). Slightly higher figures for manganese are undoubtedly due to the presence of ripe ovaries in the July samples. It has been shown by Galtsoff (1942) that ovaries store a relatively large amount of manganese and seasonal fluctuations of this metal in oysters coincide with their sexual cycle.

Greenish discoloration of tissue is probably associated with increased copper content, which may be responsible for their disagreeable and somewhat bitter taste. It is, however, of interest to note that green oysters of Long Island Sound have a much higher copper content, often exceeding 2,000 milligrams per kilo. In comparison with these oysters, the copper content of the York River oysters is rather low. The reason for the greater accumulation of metals by the oysters in the upper York River, as compared with those from its lower part, is not clear. There is apparently no excess of heavy metals in the pulp-mill effluent and it is, therefore, doubtful whether the increased amount of metals in the oyster meats comes from the pulp-mill wastes. Their accumulation is probably the result of the metabolic disturbances which interfere with the excretion of metallic salts. This problem requires, however, special study which could not be undertaken in the course of the present investigation.

QUALITY OF YORK RIVER OYSTERS AS DETERMINED BY THE SO-CALLED CONDITION FACTOR

The quality of oysters can be measured by determining the ratio between the dry weight of the meat and the volume of the cavity (in milliliters) of the shell. The idea was originated by Caswell Grave (1912), who expressed the "fatness of oysters" by determining the percentage of the shell cavity filled with meats. Hopkins in 1937 (Higgins 1938) showed that the ratio

$$\frac{100 \times \text{dry weight in grams}}{\text{Volume of cavity in milliliters}}$$

is a very useful index of the quality of oyster meat. Since that time this index has been extensively used by shellfish investigators on the west coast and in Canada.

In order to determine the relationship of shell cavity to total volume of shell, and of the meat to shell cavity, of oysters in the York River, samples of 100 oysters each were collected from station 20 in the lower York and station 16 in the upper York. Observations were made during the last of May and the first of June 1937.

After the oysters were scrubbed clean with a wire brush, they were weighed individually to the closest tenth of a gram. Each oyster was placed in a celluloid box partly filled with water, having a glass-tube side arm, and the displacement was measured. This container was 5 by 4.5 by 9.5 centimeters, and the glass tube at the side was of 6 millimeter bore, graduated in 10 cubic centimeter units. The oysters were then opened carefully and the meats dried individually in an electric oven at 50° C. for 4 days, and at 100° C. for 1 day, and the weight of the dried material determined. The weight of the two valves of each oyster was determined, as was also the volume by displacement. The shell-cavity volume was then determined by finding the difference between the volume of the whole oyster and the volume of its shell. The results were averaged for each sample of 100 oysters and are presented in table 35.

From these observations it is apparent that the shell comprises 80 percent of the total weight of the oysters of the lower York and 73 percent of the total weight of those of the upper York. The shell cavity constitutes 34 percent of the total volume of the lower river oysters and 47 percent of the total volume of those of the upper. However, there is

TABLE 35.—*Relationship of volume and shell cavity of oysters in the lower and upper York River*

[Results are averages from 100 oysters at each locality]

Locality	Total weight in grams	Shell weight in grams	Total volume, cubic centimeters	Shell volume, cubic centimeters	Cavity volume by difference, cubic centimeters	Dry weight of meats, grams	Condition factor
Lower York River	147.6	118.5	81.9	53.8	28.1	2.34	8.32
Upper York River	75.6	55.1	45.5	24.1	21.4	1.26	5.88

29 percent more meat in the cavity of the oysters of the lower York, if we compare the factors obtained by dividing the dry weight by the volume of the cavity, thus:

$$\text{Lower York River: } \frac{\text{Dry weight of meats}}{\text{Volume of cavity}} = 0.08318 \text{ gm./cc.}$$

$$\text{Upper York River: } \frac{\text{Dry weight of meats}}{\text{Volume of cavity}} = 0.05885 \text{ gm./cc.}$$

These data confirm the observations that the shells of the upper York River oysters are thinner than the shells of those from the lower part of the river. The shell cavity of the oyster of the upper York River is, however, greater than that in the oyster of the lower part, but the greater volume of shell space contains less meat because of the higher water content of the oysters in the upper part of the river.

GLYCOGEN CONTENT OF OYSTERS

The glycogen content of the oyster fairly expresses the quality of its meat and furnishes a possibility of evaluating the condition of the oyster in definite quantitative terms. The purpose of the observations described in this section was, first, to study the glycogen cycle in native oysters found at different stations in the York and the Piankatank Rivers; second, to determine the effect of transplantation of James River oysters, known to be in good condition and growing in areas of good environment, to the York River; and third, to determine the effect of the removal of oysters from the badly affected areas of the upper York River and their transplantation to areas in the lower part of the York and the Piankatank Rivers, known to be favorable to good oyster production. It was expected that the proposed studies, if carried on over a sufficiently long period, would provide definite answers to the following questions: Is the upper York River environment decidedly adverse to newly planted healthy oysters? Will removal from the upper part of the York River to a better environment restore the normal conditions of the affected oysters?

Cycle in the Oysters of the York and Piankatank Rivers

For a study of the glycogen cycle of the oysters of the York River, a sample of 25 oysters was taken each month from native beds at designated stations. These stations were selected as being more or less evenly spaced up and down the river and were located on both sides. From November 1935 to April 1937 samples were procured from stations 20, 14, 5, and 9 in the York River and from stations 55 and 53 in the Piankatank River. After July 1936, samples from stations 23, 6, and 8 in the York River were added.

After the oysters were brought to the laboratory, they were carefully opened and the meats allowed to drain on a double thickness of paper toweling for 15 minutes. The meats were then passed twice through a food grinder, and a sample of approximately 10 grams of the ground meats was taken and carefully weighed in a covered dish. The glycogen content was then determined according to the method of Pflüger (1906), as described in detail in the handbook of methods, Association of Agricultural Chemists (1935) and with the titration of sugar according to the method of Hagedorn and Jensen (1923). Computation of the glycogen from the sugar titration was made by the usual conversion factor of 0.9. The results were expressed in percentage of glycogen of the sample on a wet-weight basis.

During the course of these studies the method of glycogen determination in oysters was critically studied by Calderwood and Armstrong, who suggested several valuable modifications that greatly expedite the procedure and increase the accuracy of the results. The suggested modifications are described in a separate paper (Calderwood and Armstrong 1941).

In table 36 are shown the results of the analyses for nine stations in the York and the Piankatank Rivers. During the winter of 1936–37 it was impossible to obtain certain samples in January and February because of the extremely cold weather and the fact that much of the upper parts of the rivers were covered with ice.

The data for three stations in the York River were selected for graphic presentation in figure 33. Station 20 represents the lower York River, station 5 the middle York River, and station 9 the upper York River. Seasonal fluctuations in the glycogen content of the oysters of the Piankatank River at stations 53 and 55 are shown in figure 34.

It will be seen that the curves for the York and Piankatank Rivers follow the same trend, differing only quantitatively. The data show that throughout the year the oysters of the Piankatank River maintained a higher glycogen content than those of the York River. Curves in figure 33 show also that the glycogen content of the York River oysters decreases from the mouth of the river toward its head. The process is reversed in the Piankatank, where oysters from the upper part of the river are richer in glycogen than those from the lower part,

TABLE 36.—*Glycogen content of oysters in the York and the Piankatank Rivers*

[Glocogen in percentage is on a wet-weight basis]

Date	York River							Piankatank River	
	Station 20	Station 14	Station 23	Station 5	Station 6	Station 8	Station 9	Station 55	Station 53
1935									
November	4.95	3.66	----------	3.30	----------	----------	3.01	5.05	4.64
December	4.88	----------	----------	----------	----------	----------	3.58	4.92	6.25
1936									
January	----------	----------	----------	----------	----------	----------	----------	4.70	6.03
March	2.67	2.84	----------	2.22	----------	----------	1.48	3.65	4.44
April	2.59	2.62	----------	2.78	----------	----------	1.52	5.59	4.83
May	4.35	3.88	----------	3.26	----------	----------	1.50	3.93	5.11
June	3.80	2.20	----------	1.91	----------	----------	1.79	2.90	6.04
July	3.04	2.29	1.12	1.56	1.03	0.68	1.38	1.70	3.00
August	2.15	2.26	1.53	1.15	1.83	.89	1.27	.67	1.69
September	2.40	1.49	.44	.67	1.25	----------	.41	1.31	1.54
October	2.91	2.58	1.48	----------	1.43	.56	.73	2.25	2.82
November	2.75	2.69	1.67	----------	2.09	.61	1.12	2.72	4.13
December	3.95	2.77	1.02	1.45	----------	----------	1.21	4.06	5.21
1937									
January	----------	2.85	2.52	2.59	2.12	1.47	1.88	----------	----------
February	4.06	3.74	2.10	2.84	2.17	1.98	1.76	5.94	5.44
March	3.70	4.61	----------	2.67	1.60	1.11	1.73	2.40	3.83
April	5.28	2.79	----------	2.35	----------	1.43	1.65	2.84	2.97
Average	3.56	2.88	1.49	2.21	1.69	1.12	1.63	3.35	4.24

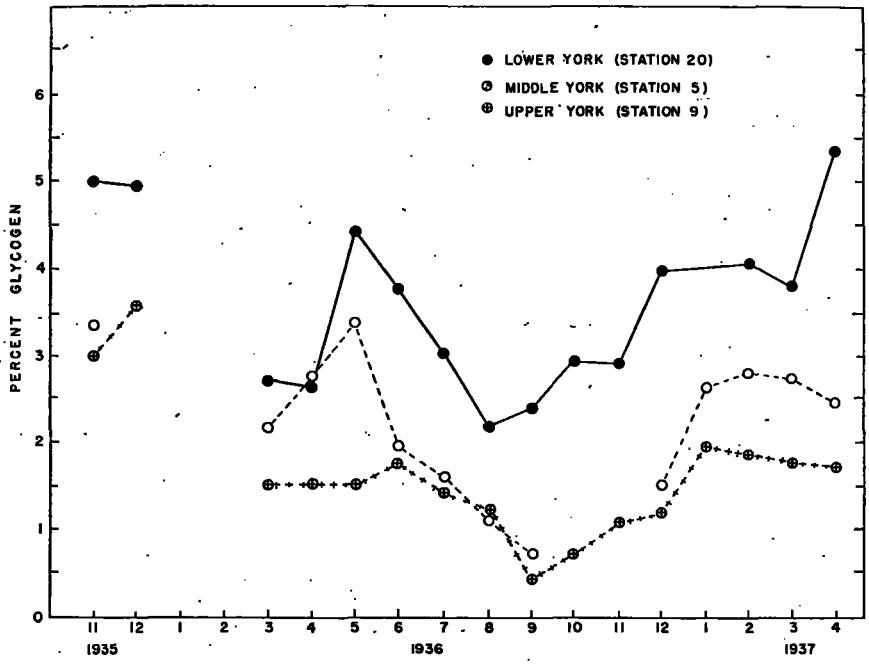

FIGURE 33.—Glycogen content of York River oysters from the lower, middle, and upper parts of the river. Glycogen in percentage is on a wet-weight basis.

although the difference is less pronounced than in the York River.

A direct correlation between the distance from West Point (upper part of the river) and the increase in glycogen content can be seen also in figure 35, which represents a 9-months' average (July 1936 to March 1937) of the glycogen content of oysters at various stations in the York and Piankatank Rivers.

Despite the fact that the average figures used in this diagram tend to diminish the extent of vertical fluctuations of the curve, it is quite apparent that oysters in the upper half of the river, above Claybank, are decidedly lower in glycogen. Marked improvement in oyster-quality occurs in the York River at stations 14 and 20 and in the Piankatank River.

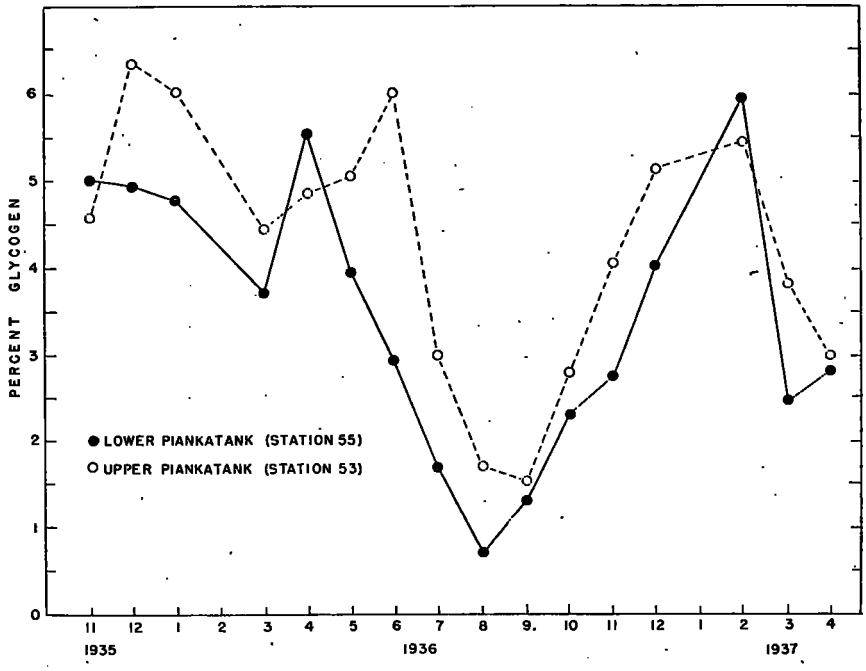

FIGURE 34.—Glycogen content of oysters from the lower and the upper Piankatank River. Glycogen in percentage is on a wet-weight basis.

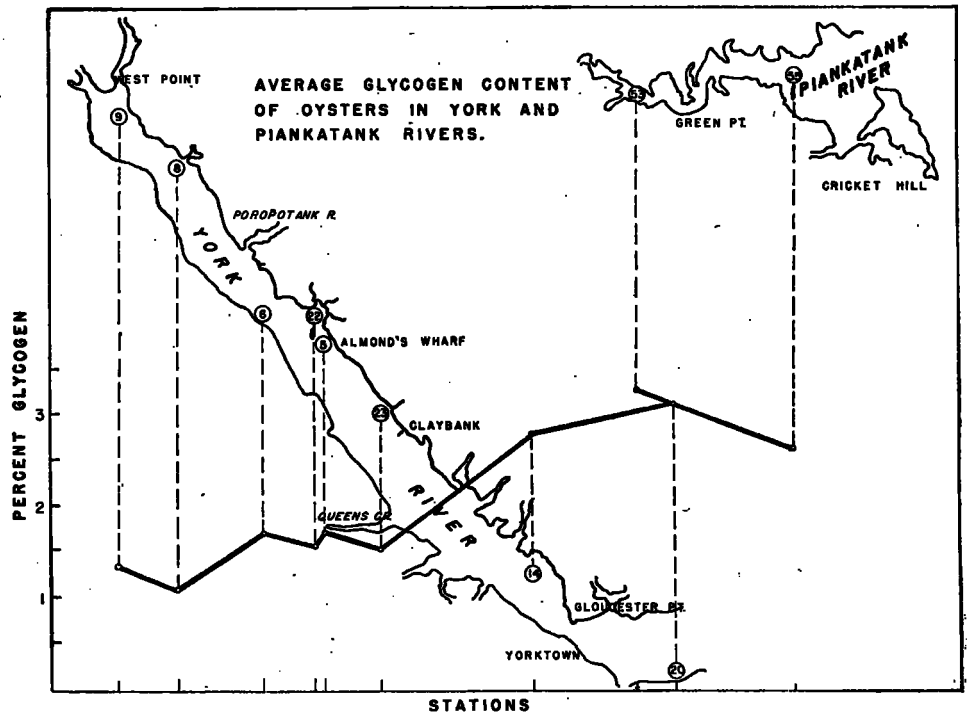

FIGURE 35.—Average glycogen content of the oysters at the various stations in the York and the Piankatank Rivers from July 1936 to March 1937, iuclusive. Glycogen in percentage is on a wet-weight basis.

Changes in the Glycogen Content of James River Seed Oysters Transplanted to the York and Piankatank Rivers

James River seed oysters were selected for transplanting experiments for their good quality and because they are generally used by the oyster growers in Virginia for planting on private bottoms. In December 1935 and January 1936 these oysters were planted at stations 20, 14, 15, 5, 16, 17, and 9 in the York River and at stations 55 and 53 in the Piankatank River. At monthly intervals 10 oysters were tonged from each station and analyzed for glycogen content. The results of these determinations for the various stations are shown in table 37.

Differences in the trend of the glycogen cycles of these oysters became apparent only 6 months after planting. This is clearly evident in figure 36, representing the seasonal changes in glycogen content of James River seed oysters transplanted to the lower York River (station 20), to the upper York River (station 9), and to the upper Piankatank River (station 53). The low glycogen content at the upper York River station during the winter of 1936–37 stands in contrast to the high glycogen level attained by oysters planted in the lower part of the York and Piankatank Rivers.

A direct correlation between the increases in glycogen content of the planted oysters in the York River and the distance from West Point is apparent in figure 37, which represents averages for 15 months at the different stations. The curve is almost identical with that based on the analyses of native oysters (fig. 35), with the difference that decided improvement in the condition of oysters becomes apparent at station 15, near Queens Creek. The difference may be easily attributed to the different locations of stations used in the two sets of observations. In contrast with the York, we again find the highest glycogen content at the upper station in the Piankatank River.

Glycogen Changes in Oysters Transplanted from the Upper York River to the Lower York and the Upper Piankatank Rivers

Low glycogen values, as illustrated by analyses of the upper York River oysters, suggested a transplanting experiment to determine whether the glycogen content would increase and reach a normal level when the oysters are removed from the unfavorable environment. If the poor condition of the oysters in the upper part of the river is primarily the result of their weakened or diseased state, one would expect them to remain poor for some time after transplanting. On the other hand, marked improvement in the meats upon transplanting the oysters to good waters would indicate that the cause of their poor condition is the unhealthy environment.

In March 1936 oysters were tonged at station 22 in Purtan Bay and transplanted downstream at station 20 at the mouth of the river, and at station 53 in the upper Piankatank River. Monthly samples consisting of 10 oysters each were taken

TABLE 37.—*Glycogen content of James River seed oysters transplanted to the York and the Piankatank Rivers*

[Glycogen in percentage is on a wet-weight basis]

Date	York River							Piankatank River	
	Station 20	Station 14	Station 15	Station 5	Station 16	Station 17	Station 9	Station 55	Station 53
1935									
December	[1] 2.70	[1] 2.70	----------	[1] 2.70	----------	----------	[1] 2.70	----------	----------
1936									
January	2.24	2.18	[1] 2.33	----------	[1] 2.33	[1] 2.33	----------	[1] 2.60	[1] 2.60
February	2.87	2.88	2.99	3.42	2.85	----------	1.78	2.96	3.39
March	2.21	2.07	1.71	2.74	1.76	1.97	2.21	2.74	3.20
April	2.30	1.70	2.66	2.68	2.34	2.28	2.41	2.80	3.12
May	1.98	1.63	2.18	2.44	1.78	3.26	1.97	2.76	3.32
June	1.85	1.41	2.06	----------	2.34	3.26	1.49	3.72	3.38
July	2.62	2.68	3.89	1.64	.40	.97	1.51	1.20	1.79
August	2.62	2.13	1.85	.89	1.06	.99	1.24	2.04	2.19
September	2.40	2.36	2.02	.88	1.34	.46	.41	1.45	1.43
October	2.60	2.64	2.46	2.34	2.47	2.00	1.77	1.88	----------
November	4.31	2.83	3.90	----------	1.69	1.92	1.17	3.21	3.70
December	5.27	2.20	----------	1.40	1.32	1.45	1.86	2.60	5.93
1937									
January	3.50	----------	3.10	2.07	1.47	1.00	1.32	3.90	4.42
February	5.66	4.20	4.24	2.78	2.50	1.92	2.43	----------	3.67
March	4.32	4.85	3.86	----------	----------	----------	----------	----------	4.07
April	4.35	2.98	4.76	3.71	2.26	3.44	1.65	----------	3.03
Average	3.16	2.58	2.97	2.24	1.82	1.95	1.66	2.60	3.29

[1] At time of transplanting.

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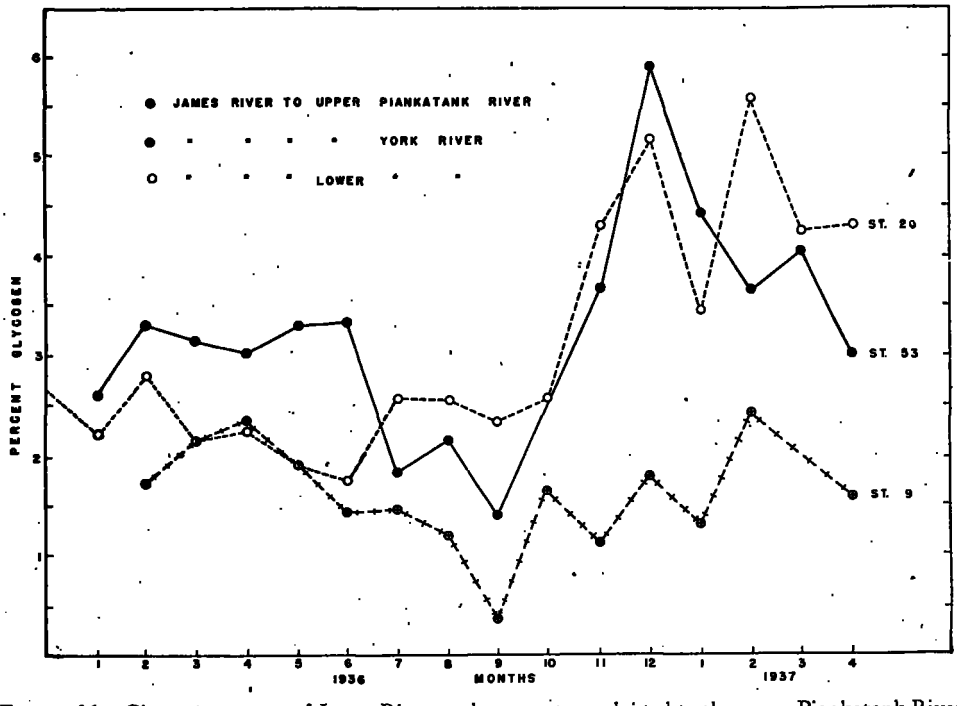

FIGURE 36.—Glycogen content of James River seed oysters transplanted to the upper Piankatank River and to the upper and lower sections of the York River. Glycogen in percentage is on a wet-weight basis.

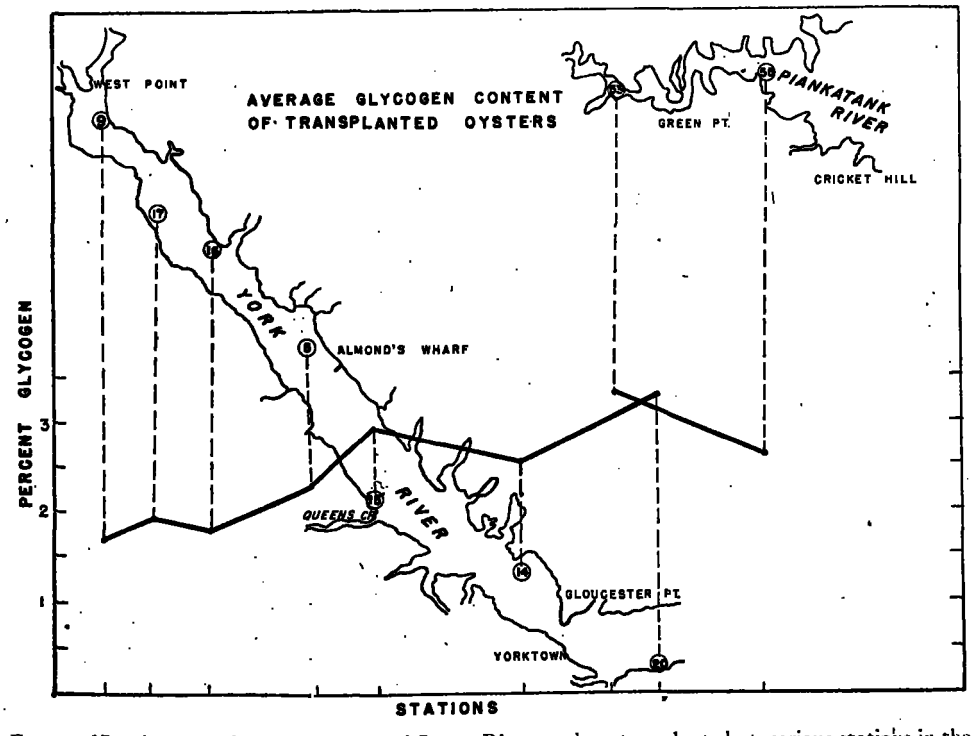

FIGURE 37.—Average glycogen content of James River seed oysters planted at various stations in the York and Piankatank Rivers. Glycogen in percentage is on a wet-weight basis.

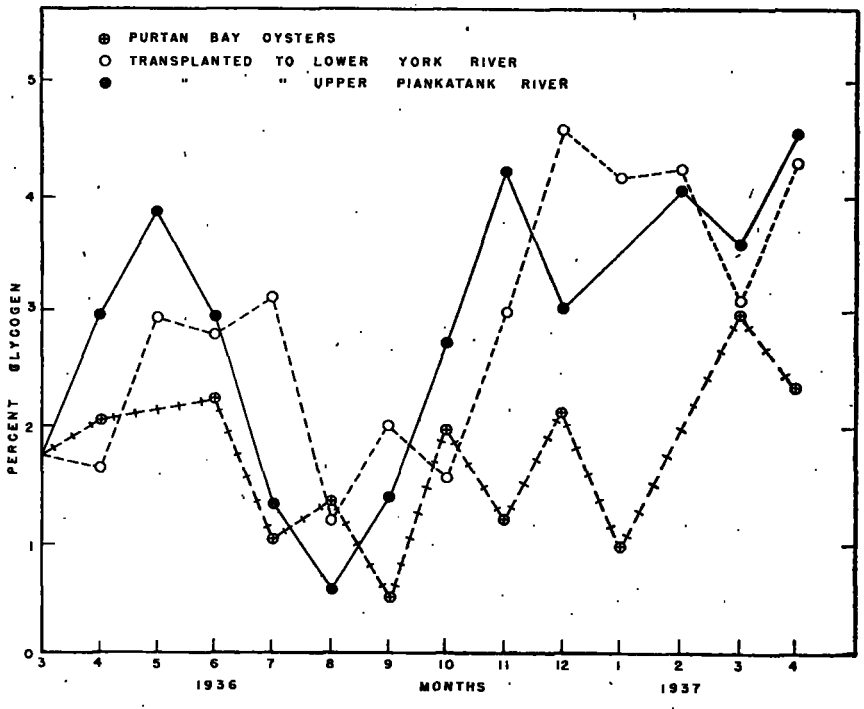

FIGURE 38.—Glycogen content of Purtan Bay oysters transplanted to the lower York and the upper Piankatank Rivers. Glycogen percentage is on a wet-weight basis.

from all 3 localities for analysis. The results of the observations extending from March 1936 to April 1937 are shown in figure 38. Almost an immediate improvement is noticeable in the condition of the oysters after their removal from Purtan Bay. During the summer months the difference disappears, only to become more pronounced in the following fall and winter.

The results of the experiments show definitely that the factors that retard glycogen formation in the York River oysters inflict no permanent injury to the organism. The action is that of a general depressant inhibiting the carbohydrate metabolism. Apparently there is no accumulation of toxic substances in the body and no irreparable injury is inflicted on the oysters kept in the upper York River, for recovery after transplanting is very rapid. The improvement in the condition of the oyster is not restricted to the increase in glycogen content; it is accompanied by an increased rate of growth, the deposition of shell material, and the disappearance of both the greenish color and the strong or acrid taste of the meat.

From the practical point of view, the results of the transplanting experiments point to the possibility of a partial solution of the oyster-cultural problem in the upper York River.

WATER CONTENT OF THE OYSTERS OF THE YORK AND THE PIANKATANK RIVERS AND OF THE VARIOUS TRANSPLANTED OYSTERS

As samples of oyster meats were being prepared for glycogen determination, a portion of the ground meats was dried and the percentage of water determined. As previously mentioned, the meats, after removal from the shell, were allowed to drain for 15 minutes on a double thickness of paper toweling and then passed twice through a food chopper. Approximately 30 grams of the ground meats were placed in a previously weighed container and the weight of the meats computed. Then, they were dried in an electric oven at 50° C. for 24 hours and at 100° C. for another 24 hours. The sample was allowed to cool in a desiccator and then reweighed.

The water content of the oysters of the York and the Piankatank Rivers was determined from the ground meats of 25 oysters taken each month from native beds at designated stations. From November 1935 to April 1937 samples were obtained from stations 20, 14, 5, and 9 in the York River and stations 55 and 53 in the Piankatank River. After July 1936, stations 23, 6, and 8 in the York River were added. The results of these observations are presented in table 38.

TABLE 38.—*Percentage of water in oyster meats from different stations in the York and the Piankatank Rivers*

Date	York River							Piankatank River	
	Station 20	Station 14	Station 23	Station 5	Station 6	Station 8	Station 9	Station 55	Station 53
1935									
November	81.6							82.5	82.0
December	80.8						83.8	81.7	79.3
1936									
January								81.1	79.2
March	82.7			80.6				81.5	79.8
April	84.1	83.1		87.0			88.8	81.4	82.9
May	82.2	82.2		83.1		87.7	87.4	83.3	80.9
June	82.6	79.7		81.7			79.0	82.8	79.3
July	77.9	78.9	78.9	82.4	81.6	79.6	82.0	83.3	82.0
August	79.9	79.0	84.8	85.1	87.9	86.5	84.0	86.2	82.2
September	81.5	86.3	86.1	86.2			86.6	86.4	84.7
October	80.7	81.4	84.5		85.2	85.7	85.3	81.0	82.8
November	83.4	82.3	85.7		84.9	87.2	85.1	81.2	77.4
December	82.6	78.9	70.3	86.1	86.7	86.4	83.6	80.7	79.0
1937									
January	88.3	83.2	84.3	91.2	91.6	85.5	83.6	83.9	79.1
February	83.4	83.0	84.1	83.3	85.2	84.2	83.7	81.7	83.0
March	83.7	82.3	86.5	86.1	87.8	87.0	86.9	83.6	82.1
April	83.1	86.2	88.7	85.7	86.5	88.5	86.8	84.1	82.8
Average	82.4	82.0	83.4	84.9	86.4	85.8	84.8	82.7	81.1

It can readily be seen that the oysters of the upper York River were more watery than those of the lower, the oysters in the lower averaging about 82 percent water and those of the upper about 86 percent. It will be noticed that the oysters of the upper Piankatank had a slightly smaller water content than those of the lower river, but the upper Piankatank River (station 53) oysters were very much less watery than those of the upper York (stations 5, 6, 8, and 9).

These analyses of water content of the oysters of the various localities are in harmony with the general observations of oyster conditions at the various places and with the "fatness" of the oysters as measured by their glycogen content. The areas having oysters of higher glycogen content also had oysters with a smaller water content.

The percentage of water found in the James River oysters transplanted to the various stations in the York and the Piankatank Rivers is given in table 39. These analyses are based on samples of 10 oysters each taken monthly from January 1936 to April 1937.

It will be seen that the water content of the oysters varied in accordance with the location in which they were planted. The oysters planted at the various stations in the York and the Piankatank Rivers be-

TABLE 39.—*Percentage of water in James River seed oysters transplanted to various stations in the York and the Piankatank Rivers*

Date	York River							Piankatank River	
	Station 20	Station 14	Station 15	Station 5	Station 16	Station 17	Station 9	Station 55	Station 53
1935									
December	[1] 82.5	[1] 82.5		[1] 82.5			[1] 82.5		
1936									
January	85.0	87.6	[1] 87.2		[1] 87.2	[1] 87.2		[1] 87.4	[1] 87.4
February	88.1	83.9	86.9	88.7	86.5		88.6	84.6	84.5
March	83.1	84.5	83.3	86.4	88.4	88.7	88.7	85.3	85.7
April	90.7	84.8	85.9	88.6	88.6	88.6	86.3	85.6	85.8
May	85.0	89.0	85.4	85.4	86.5	86.7	86.3	85.3	83.8
June	92.6	83.2	81.5	81.1	88.3	88.6	86.4	82.1	86.6
July	73.0	78.7	80.3	78.4	84.7	82.2	83.7	76.5	84.9
August	80.7	81.5	78.4	84.6	86.1	84.2	83.2	84.9	82.9
September	79.1	81.4	81.2	86.6	85.7	85.4	86.5	86.4	85.1
October	81.5	83.5	84.2	80.4	83.0	83.6	84.2	87.7	81.7
November	79.8	78.5	79.7		84.9	85.2	82.2	80.2	79.6
December	80.9	81.3	80.1	85.2	84.5	87.2	81.9	84.0	79.4
1937									
January	87.3	81.7	82.7	90.9	85.3	86.7	91.2	84.2	81.0
February	80.9	82.4	84.5	83.3	84.0	86.0	83.7		83.8
March	80.7	81.1	81.8	85.3	86.1	84.6	86.2		83.2
April	82.5	84.3	82.2	84.4	86.5	85.4	86.5		82.8
Average	83.2	83.0	82.5	85.0	85.9	86.0	85.7	83.9	83.4

[1] At time of transplanting.

came similar in water content to the oysters already there. The oysters planted in the upper York River became much more watery than the oysters planted elsewhere. It will be noticed that in the Piankatank River the oysters had nearly the same water content as those in the lower York, and that the oysters of the lower Piankatank were slightly more watery than those from the upper part.

In order to observe the effect of transplanting poor oysters to areas known to produce good oysters, the following experiment was carried out. In March 1936, oysters were tonged from station 22 in Purtan Bay and transplanted downstream at station 20 at the mouth of the river and at station 53 in the upper Piankatank River. Monthly samples consisting of 10 oysters each were taken from all 3 localities for analyses. The results of observations of water content from March 1936 to April 1937 are shown in table 40.

The results show an improvement in the water content of the oysters after their removal from Purtan Bay. Those remaining in the original bed were much more watery throughout the time of observations than those removed to a different environment. This improvement is in line with the improvement in general condition and in glycogen content as previously noted.

Transplanting experiments show that with respect to general condition, water content, and glycogen content, the transplanted oysters within a short time acquire the characteristics typical of native oysters.

TABLE 40.—*Changes in water content of oysters transplanted from station 22 in the upper York River to the lower York and the upper Piankatank Rivers*

Date	Not transplanted Upper York (station 22)	Transplanted	
		Lower York (station 20)	Upper Piankatank (station 53)
1936			
March	86.9	[1] 86.9	[1] 86.9
April	85.6	83.4	86.5
May	84.1	83.8	83.6
June	83.3	82.9	83.7
July	82.5	77.5	84.6
August	84.5	81.0	83.2
September	87.7	82.1	86.5
October	85.3	81.2	81.4
November	85.6	81.4	78.5
December	83.4	81.4	79.5
1937			
January	91.8	88.5	81.0
February	89.8	83.0	83.0
March	85.9	83.2	83.1
April	82.0	----------	82.8
Average	85.5	82.4	82.9

[1] At time of transplanting.

BIOLOGY AND CULTIVATION OF THE OYSTER IN THE YORK RIVER

Studies of the biology and cultivation of the oyster in the York River were carried out in 1936 and 1937 for the purpose of determining practical procedures that might be helpful in overcoming the increasing difficulties of the oyster growers. The history of the industry of this area indicates that the York River is primarily an oyster-growing area that produces but little natural set. The many bushels of market-oysters harvested in the past from this river came principally from planting seed oysters obtained elsewhere, mostly in the James River. The density of planting varied from 500 to 1,500 bushels an acre, depending on the type of bottom and the size of the seed. According to statements made by local oystermen still engaged in the business of growing oysters in the York River, the yield in the upper part of the river prior to 1918 varied from 1 to 3 bushels for each bushel planted. Most of the grounds at the time of this investigation did not produce more than one-half bushel for each bushel of seed planted. The period required to grow the seed to marketable size varied from 18 months to 3 years, depending on the location of the planting and the size of the seed when planted.

The continued poor condition of the oysters and their unmarketability had discouraged the planting of seed, with the result that, at the time of these studies, old oysters were predominant on the grounds with only small numbers of spat or seed present.

The last set of oysters of commercial value, according to the planters, occurred in 1933. Marketable oysters were harvested only in the lower part of the river where some planting operations were still continued.

GONADS

Observations on the development of the gonads were started at the end of June 1936 and continued to June 1937. Oysters in the lower part of the river ripened earlier than those above. During June 1936, from 80 to 100 percent of the oysters examined at stations 14 and 20 had fully developed and ripe sex products, while the oysters at the stations farther up the river showed a lesser degree of ripeness. In 1937 an examination made during the last week of May disclosed, in general, the same situation, with 60 to 80 percent of the oysters of the lower part of

TABLE 41.—*Condition of the gonads in oysters in the York River during 1936 and 1937*

[Stations arranged from lower to upper river]

Station No.	June 26, 1936				Sept. 26 to Oct. 1, 1936				Nov. 4 to 6, 1936				Mar. 4, 1937				May 24 to June 7, 1937			
	Number examined	Undeveloped	Partly developed	Ripe	Number examined	Undeveloped	Partly developed	Ripe	Number examined	Undeveloped	Partly developed	Ripe	Number examined	Undeveloped	Partly developed	Ripe	Number examined	Undeveloped	Partly developed	Ripe
20	10	0	0	10	14	0	6	8	10	1	0	9	10	9	1	0	15	0	4	11
14	10	0	2	8	13	0	10	3	10	0	3	7	10	4	6	0	20	1	7	12
15	10	4	2	4	0	------	------	------	10	3	1	6	10	10	0	0	22	2	4	16
23	10	2	8	0	0	------	------	------	0	------	------	------	10	7	3	0	20	3	16	1
5	10	0	5	5	15	10	4	1	0	------	------	------	10	9	1	0	20	1	18	1
6	10	0	7	3	11	4	4	3	0	------	------	------	10	10	0	0	0	------	------	------
17	0	------	------	------	0	------	------	------	7	0	4	3	0	------	------	------	0	------	------	------
16	10	5	5	0	0	------	------	------	0	------	------	------	0	------	------	------	0	------	------	------
22	0	------	------	------	0	------	------	------	0	------	------	------	10	8	2	0	20	0	13	7
8	10	0	9	1	14	7	2	5	0	------	------	------	0	------	------	------	0	------	------	------
9	10	1	4	5	15	3	5	7	13	3	7	3	7	6	1	0	0	------	------	------
24	10	0	9	1	0	------	------	------	0	------	------	------	0	------	------	------	0	------	------	------
Total	100	12	51	37	82	24	31	27	50	7	15	28	77	63	14	0	117	7	62	48
Percentage	------	12	51	37	------	29	38	33	------	14	30	56	------	82	18	0	------	6	53	41

the river containing ripe gonads, while in the upper part of the river only 5 to 30 percent of the oysters were ripe. Throughout the summer and fall some oysters with ripe gonads always were present and only during the winter and early spring were oysters found without functional gonads. Of the oysters examined in March 1937, 82 percent had no gonad material discernible with the naked eye and no specimen contained mature sex products, although 18 percent of the oysters were found to have small amounts of sex products. These could be considered either as the beginning of the development for the coming spawning season or as the remnants of sex products not yet absorbed (table 41).

SPAWNING AND OCCURRENCE OF LARVAE

In 1937 fully ripe gonads were first observed during the latter part of May. Judging by the subsequent changes in the appearance and consistency of the gonad tissues, it may be concluded that spawning started during the same time. Straight-hinge oyster larvae were found in plankton from June to November. Using their number as a criterion of the intensity of spawning, it was found that reproductive activities of oysters were more pronounced in the lower part of the river than in its upper section, although some spawning took place on all the grounds of the river bottom.

During the spawning season of 1936, frequent plankton samples were taken by means of a 45-liter plankton trap. The sample was concentrated to 10 cc., preserved in 10 percent formaldehyde, and the oyster larvae counted in a Sedgwick-Rafter cell. In sampling the river, 3 or 4 days were usually required to complete a cruise. For convenience in summarizing these data the river was arbitrarily divided into three sections, lower, middle, and upper. In recording the abundance of oyster larvae, the straight-hinge larvae were considered as recently spawned, the umbo larvae represented those which had passed about two-thirds of the larval period, and the "eyed" larvae were those of the very late stage, immediately preceding the setting.

Straight-hinge larvae were present in all the samples taken from June 16 through November 3, 1936, but the eyed larvae were scarce, and in most samples absent. This is an occurrence frequently noted by American biologists engaged in oyster studies.

The mean number of larvae per 45-liter sample taken at each of the stations in York River showed a greater abundance in the lower section of the river and a gradual diminution as one proceeds upstream (table 42). This can be easily seen in figure 39, which shows the results of counts made of samples collected during one cruise at station 14, lower section, station 5, middle section, and station 9, upper section. Three major peaks of intensity of spawning occurred during this season: the first, of the longest duration, was noticed during the first half of July, the second, of short duration, occurred about the middle of August, and the last, also of brief duration, took place about the first of October. Oyster larvae disappeared from the plankton early in November.

It was apparent from the examination of plankton samples that the number of oyster larvae rapidly decreased as one proceeded from the mouth of the river upstream. This condition is clearly shown in

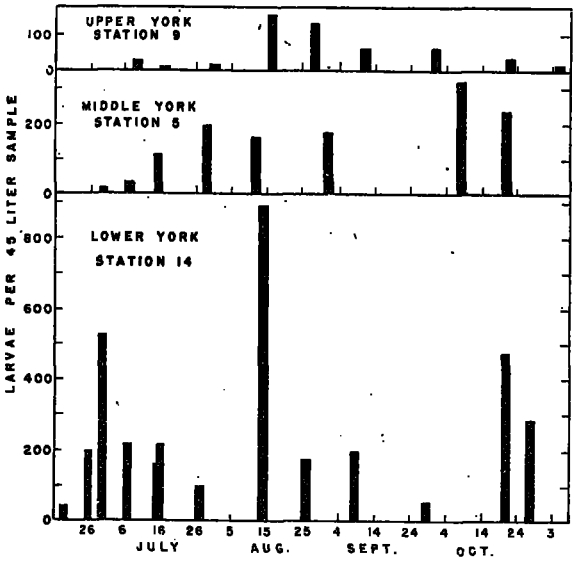

FIGURE 39.—Seasonal occurrence of oyster larvae at three stations in the York River, 1936

figure 40 representing the mean number of larvae in samples collected throughout the season at three sections of the river. The number of samples collected at each section was as follows: in the lower part, 31 samples at 3 stations; in the middle part, 32 samples at 4 stations; and in the upper part, 37 samples at 4 stations. The decrease in the number of oyster larvae was probably due to some abnormal condition of the environment in the upper part of the river because spawning and setting in tidal waters frequently takes place in water of reduced salinity.

TABLE 42.—*Mean number of free swimming larvae per 45-liter sample in the York River*

Lower river			Middle river			Upper river		
Station No.	Number of samples	Number of larvae	Station No.	Number of samples	Number of larvae	Station No.	Number of samples	Number of larvae
20	9	648	23	8	165	16	9	52
14	13	273	5	9	163	17	9	90
15	9	230	22	8	175	8	8	78
			6	7	50	9	12	50
						18	[1] 7	14
						19	[2] 7	38

[1] Pamunkey River.
[2] Mattaponi River.

SETTING OF OYSTERS IN 1936

During the summer and fall of 1936, wire bags filled with shells were placed at several stations in the York River to obtain information on the period and intensity of oyster setting. The shells, obtained from a local shucking house, had not been used previously as cultch. It was certain, therefore, that any spat, or scars showing the place of the attachment of spat, had attached or been formed during the period of exposure of the shells at the selected stations. Bags were taken out and replaced by new ones at intervals of 2 to 4 weeks. Fifty shells, taken from each of the bags, were examined with a dissecting microscope and the number of spat on the inner surface of the shalls counted. From the data thus obtained, the number of spat per bushel of shells was computed. Because the interval between the observations sometimes was too long to determine the exact time of setting, the approximate time was estimated by measuring all spat found on the shells, and plotting an age-distribution curve for the period of the exposure of the bag of shells. Using this method, first suggested by Hopkins (1931), the approximate times of major setting-periods were determined and plotted (fig. 41).

The first collectors were placed on June 11 at several stations in the lower and middle parts of the river. The first set appeared about July 15 at station 14 opposite Yorktown. After this date, setting of varied intensity occurred throughout the summer until October 19. In the lower part of the river, two periods of relatively heavy setting were recorded (fig. 41), the first during the last half of July and the early part of August, and the second about the middle of September. The latter setting was the heaviest and was almost of commercial importance. Each of the two peaks of heavy-setting periods occurred approximately two weeks after the corresponding periods of abundance of the oyster larvae.

The setting of oysters in the upper section of the

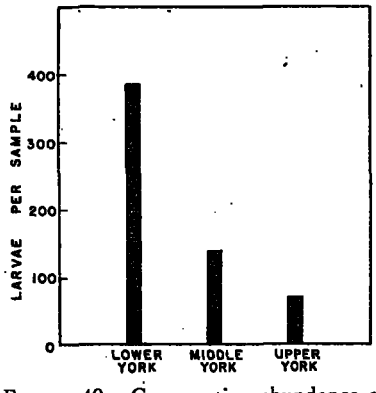

FIGURE 40.—Comparative abundance of oyster larvae in the three sections of the York River. The columns represent the mean number of larvae per sample, for the period from June 16 to November 4, 1936.

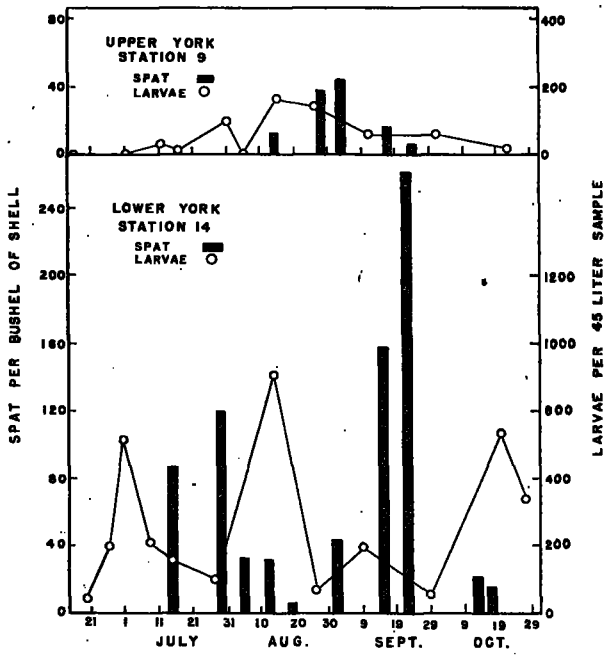

FIGURE 41.—The occurrence of larvae and setting of oysters at two stations in the York River, June to October 1936.

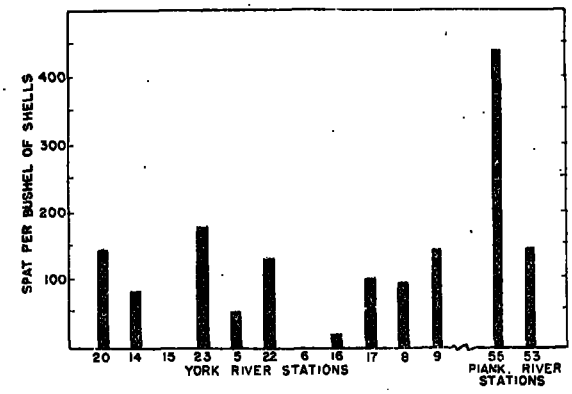

FIGURE 42.—Number of oyster spat per bushel of oysters and shells taken from the bars in the York and the Piankatank Rivers at the end of the setting season, 1936.

York River during 1936 was considerably less than that in the lower part, and of shorter duration. The first setting was recorded during the early part of August and extended through September. Station 9, near West Point, Va., was the uppermost location where shell bags were placed. Some of them were lost but enough were recovered to show that the intensity of setting was insignificant and could not provide a natural replacement of oyster populations on the bars used for commercial fishing. At station 9 scattered setting occurred during August and September and the period of heaviest setting took place during the latter part of August and early in September (fig. 41). Again the peak of larval occurrence preceded the heaviest setting by about 2 weeks. At station 14 the total number of spat per season per bag was 1,402; at station 22, near Purtan Bay, 660; and at station 9, only 226.

Data resulting from the examination of shell bags show that the setting in the York River decreased from the mouth to the head of the river. A different result was obtained, however, from an examination of natural shells and oysters on the bars of the river. In checking the number of spat per bushel of bottom material, it was found that the mortality among the spat in the lower part of the river was so great that the advantage of heavier setting in the lower part was lost. Consequently, by the end of the setting season there was no material difference between the number of spat in the two parts of the river (fig. 42).

Although the spat survived better in the upper part of the river, the intensity of setting there was too low to be of commercial value. The loss of spat in the lower part was primarily caused by the depredations of the screw borers or oysters drills, *Urosalpinx* and *Eupleura*, which abounded on the bars of the lower section of the river but were not found in its upper part. Production of seed oysters on a commercial scale appears to be feasible in the lower part of the river only if effective drill control measures are employed.

Piankatank River

The condition of gonad development, spawning, and setting in the Piankatank River resemble those in the lower and middle York River. The number

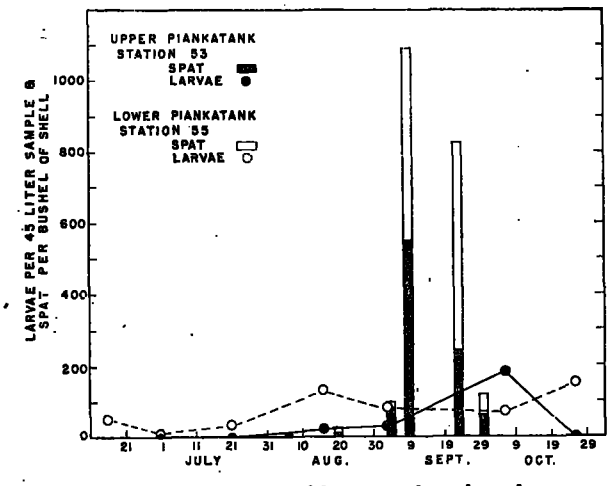

FIGURE 43.—The occurrence of larvae and setting of oysters at two stations in the Piankatank River, June to October 1936.

of larvae found in the plankton samples was smaller and varied less than in the York River. The larvae reaching setting stages were more numerous with the consequent higher rate of setting (fig. 43).

Examination of plankton samples and of shell bags were conducted at station 55, near the mouth of the river, and station 53, several miles from the mouth. The setting of oysters at each of these stations could be considered of commercial value.

ORGANISMS FOUND IN ASSOCIATION WITH OYSTERS IN THE YORK RIVER

No attempt was made to collect and identify all the forms that may be inhabiting the York River. Attention was paid, however, to the presence and abundance of organisms intimately associated with the oyster or constituting a definite danger to the oyster industry.

Sponges most common on the oyster beds in the York River were the sulfur sponge, *Cliona celata*, red bearded sponge, *Microciona prolifera*, and one unidentified species of siliceous sponge occurring in the lower part of the York River. The sulfur or boring sponge was very thickly spread in the lower river and caused considerable damage to oysters by weakening the shells. It was found as far up the river as station 9, which was probably the extreme range of its distribution in brackish water. The range and abundance of *Microciona* was the same as that of the sulfur sponge. *Microciona* constituted a nuisance to the oystermen because occasionally it caused a painful rash on the hands and arms of the men handling oysters.

Hydroids, *Thuiaria* sp., called by local watermen "moss," were abundant in the lower and middle parts of the York River.

Among other coelenterates the most common were the three genera of jellyfish, *Dactylometra quinquecirrha*, the most abundant, the red-colored *Cyanea* sp.; and *Aurelia* sp. The first two species, found only occasionally, were distributed throughout the whole river, while the last was confined mostly to the middle and lower parts. Sea anemones were seen on many of the shells and oysters brought in from all parts of the river.

Several species of Ctenophores were present, sometimes in enormous numbers. The identity of only one of them was established as *Mnemiopsis gardeni*.

An unknown turbellarian worm was found in rather great numbers on oyster shells and on oysters in the middle and lower parts of the York River.

The nemertean worm, *Cerebratulus lacteus*, was common in the river below Yorktown. It was found both in the shallow waters inshore and among the oysters in deeper water, fragments being brought up frequently in the oyster dredge.

Bryozoan colonies encrusted the shells of oysters and other animals in all parts of the river. They fouled the shell surfaces to such an extent that space available for setting of oyster larvae was greatly reduced. Undoubtedly, they were responsible in part for the light set of oysters during the summer of 1936.

The clam worm (*Nereis limbata*, Ehlers) was common throughout the river. The tubes of another annelid, tentatively identified as *Hydroides hexagonus*, often were found on the shells of oysters from all parts of the river. One planter reported that in 1935 the tube worm was thick enough to form a crust on the oysters in certain parts of the upper river. Another annelid frequently found on oyster shells was a bright red terebellid, *Polycirrus exinuis* Leidy.

The shells of the oysters contained numerous mud blisters, averaging five per shell, made by various species of *Polydora*. Live *Polydora* could be found frequently. Examination of the large number of oysters collected on July 25, 1940, along the entire length of the river showed that about one-third of the blisters contained live worms which were identified by Dr. Olga Hartman as *Polydora ligni* Webster, most common in the sample, *Polydora calca* Webster, and *Polydora* sp., probably *anaculata* Moore. Since *Polydora* blisters were found both in good and very poor oysters, it was impossible to correlate their presence or absence with the condition of the oyster.

In view of the reports by Kudo (1939) and Prytherch (1940) that mud crabs are primary hosts of the gregarine *Nematopsis* and are responsible for the distribution of this parasite on oyster beds, a survey was made of the occurrence of these crabs (family Xanthidae) in the York River. The distribution of the various species,[6] is presented in table 43, which shows the stations and the number of specimens found in a bushel of bottom debris.

The blue crab, *Callinectes sapidus*, which also may be one of the hosts of *Nematopsis*, occurred in all parts of the York River, but was more abundant in the lower section.

Filling the shells of gastropods were many hermit crabs. Their distribution was limited to the middle

[6] Dr. Mary J. Rathbun kindly identified these species.

TABLE 43.—*Distribution of mud crabs (Family Xanthidae) in York River, Va.*[1]

[Number of crabs found per bushel of bottom debris]

Station	Eurypanopeus dissimilis	Panopeus herbstii		Neopanope texana texana	Rhithropanopeus harrisii
		Typica	Simpsoni		
20	15	1		17	
14	31	1	10		
15	1				3
23	7				15
05	20				
22	23				
06	8	1			5
16	8				
08	2				14
09	6				7

[1] The samples were collected in the fall of 1936 from Oct. 7 to Nov. 6. An oyster dredge catching about ½ bushel to a drag, and a pair of tongs catching about ½ of a bushel to a grab, were used to gather the bottom material. The number of crabs were counted in the material brought up and the amount of material closely estimated.

and lower parts of the river. Spider crabs, *Libinia dubia*, and *L. emarginata* were often seen in the dredge loads taken in the lower parts of the York. Along the low banks from the mouth to the head of the river were fiddler and sand crabs. The sand crab, *Ocypode albicans*, was more abundant on the shores below Yorktown than in the upper part of the river.

Barnacles were widely distributed the length of the river and in many places completely encrusted the shells of oysters. However, they did not constitute any serious menace to the oyster industry.

The oyster crab, *Pinnotheres ostreum* Say, was observed many times in the mantle cavity of oysters opened in the course of the investigation. These crabs were found on all oyster grounds, but were more abundant in the lower part of the river. On one occasion 575 oysters were examined and 17 were found infested by crabs.

Gastropods were numerous with the greatest variety of species found in the lower part of the river. The mud snail, *Nassa* sp., abounded in the river predominating in its lower half. On the pilings and sides of moored barges in the vicinity of West Point, periwinkles, *Littorina* sp., were occasionally seen. These may have been brought in by the barges carrying pulp wood to the Chesapeake Corporation plant at West Point. No oyster drills, *Urosalpinx* sp. or *Eupleura* sp., were found in the upper river, but both species were present and constituted a serious menace in the lower part of the river. Other gastropods common in the lower part included the sand collar, *Polynices* sp., the conchs, *Busycon carica*, and *B. canaliculatum; Purpura* sp.; and several species of *Crepidula*. One of the horse mussels, *Modiolus demissus*, was abundant on the oyster beds from the mouth to the head of the York River. The edible mussel, *Mytilus edulis*, was common in the lower part of the river. Fairly abundant in the vicinity of Yorktown was the razor clam, *Ensis directus*. Several shells of oysters dredged from the lower river were found drilled by boring clam *Diplothyra* sp. This clam only rarely was found and did not constitute an oyster menace in Virginia waters.

It might be mentioned that only one specimen of starfish, *Asterias forbesi*, was taken within the lower part of the river. At the mouth of the river, however, starfish occurred in exceptional abundance in the spring of 1937 and later disappeared.

The tunicate, *Molgula* sp., occurred throughout the river. It was found growing in such thick clusters at some locations in the lower river that it completely hid the oysters to which it was attached.

In résumé, ecological observations failed to disclose the predominance of any predatory or commensal organisms which might have been responsible for the poor quality of the oysters. The animals found in York River frequently occur on oyster bottoms and can be considered as constituting a normal community of organisms inhabiting these bottoms.

EXPERIMENTAL STUDIES

Pulp-mill effluents emptied into the upper York River in large quantities constitute the only industrial pollution of the river. Physiological experiments carried out at the Yorktown laboratory were, therefore, primarily concerned with the effect of these wastes on oysters and on oyster food-organisms. Simultaneously with these observations, studies were made on the chemical nature of polluting effluents and their fractions. Physiological effect of each of the effluents and later on various fractions of them, prepared by the chemist, were tested individually or in combinations. These studies included observations on the effect of pollutants on the adductor muscle (determination of the number of hours the shells remain open), studies of the changes in the activity of the ciliated epithelium of the gill (drop-counting method), and determinations of the rate of water filtration of oysters kept in various concentrations of pollutants.

Although the literature on water pollution by pulp- and paper-mill wastes is very voluminous, the effluents from the sulfate pulping process have often been dismissed with the statement that sulfate mills do not discharge a waste liquor to pollute water

(Kobe 1937). As early as 1908 European workers began studies on the toxicity of sulfate pulp-mill effluents upon fish life (Ahlin 1908) and within the past decade extensive studies have been made upon the resin acids present in sulfate pulp-mill effluents. This recent work (Ebeling 1930, 1931, 1932; Vallin 1935; Hagman 1936; Järnfelt 1936; Bergström and Gederquist 1937; Vestergren 1938; Erdtman 1939) has been carried out chiefly in Sweden and Finland upon the finned fishes inhabiting fresh waters. All of the work has been upon the wash waters from the sulfate pulping process which contained a sufficient quantity of the resin acids to be injurious to the animals tested.

In the United States some toxicity studies have been made with the alkyl mercaptans (Cole and Warrick 1935; Cole 1935) known to be formed in the sulfate pulping process. These studies were also conducted on fresh-water fishes.

With possibly a single exception (Anon., 1910) no record was found of the effect of sulfate pulp-mill effluents upon either marine fishes or sea water. The publication in question was confined to a report on the study of the toxicity of alkali metal sulfides on fishes.

As far as could be ascertained no investigations other than the work reported here and presented in a preliminary report (Galtsoff, Chipman, Hasler, and Engle, 1938) has been made with reference to the effect of sulfate pulp-mill effluents upon oysters.

DESCRIPTION OF THE PROCESSES EMPLOYED BY THE CHESAPEAKE CORPORATION AND LOCATION AND DESCRIPTION OF THE VARIOUS SEWER OUTLETS

A description of the processes employed in manufacturing pulp and paper appears to be essential for an understanding of the nature of the effluents entering the York River and of the samples used in testing.

The mill makes its pulp from wood by the sulfate process using chiefly loblolly pine (*Pinus taeda* L.). In this process the pine chips are cooked at elevated temperatures and pressures in a water solution containing sodium sulfide and caustic soda. These chemicals dissolve the noncellulosic portion of the chip leaving the cellulose as a fibrous pulp which is separated from the cooking liquor and then purified. The separated liquor, after being fortified with chemicals from the recovery house, is reused in the cooking operation.

Before going to the paper-making machine the raw pulp from the digester is purified by counter-current washing in a diffusion apparatus. This method reduces the volume of water needed and gives increased recovery of the chemicals used for cooking the chips. The first wash water, richest in chemicals, is designated "weak-black liquor" and is sent to the recovery house for reclaiming. The last wash water, although dark in color, is too poor in chemicals for profitable recovery and is discharged into the river. The intermediate wash waters are reused, being finally withdrawn from the circuit as weak-black liquor. After removal from the diffusers the pulp is subjected to screening and further washing with paper-machine waste water, which contains very small amounts of chemicals.

The weak-black liquor, after filtration to remove suspended fibers, is concentrated in multiple effect vacuum evaporators until the "sulfate soap" begins to separate. After removal of the soap, concentration of the liquor is continued until it becomes combustible and it is then sent to the incinerators. Prior to incineration the chemicals lost in the pulp wash waters are replaced by the addition of "salt cake," sodium acid sulfate. If the sulfate soap, removed during concentration of the black liquor, cannot be sold, it also goes to the incinerator.

During incineration the noncellulosic constituents of the wood, present as soluble substances in the black liquor, burn and pass out of the smokestack as gases and vapors, leaving an ash composed chiefly of water-soluble substances, sodium carbonate and sodium sulfide, derived from the sodium compounds present originally in both the black liquor and the salt cake. The ash is dissolved and this solution is treated with quicklime which changes the sodium carbonate of the ash to caustic soda and leaves the sodium sulfide unaltered. The quicklime changes to calcium carbonate, which being insoluble, settles out as a sludge and is removed, leaving the clear solution of caustic soda and sodium sulfide to be used for cooking the wood chips.

The calcium-carbonate sludge contains appreciable amounts of the above-mentioned chemicals which are removed by a system of counter-current washing and filtration. These wash waters are used for dissolving the ash, while the washed calcium carbonate is converted into quicklime. Prior to 1935 the calcium-carbonate sludge was pumped into a fresh-water swamp, now about one-third to one-half mile from the Pamunkey River, but since then

all of the calcium-carbonate sludge, after being washed, has been reburned to quicklime, supplying from 90 to 95 percent of the quantity needed for causticizing the ash.

Due to the limited supply of process waters the fiber losses, as reported by the mill chemist, are very small. With a daily output of 350 tons of pulp, the losses are usually less than 300 pounds per day, and only rarely exceed 500 pounds per day.

The effluents from the mill are carried in various sewer lines. Their location, size, and nature of material carried have been given in figure 4, and described in pages 97–99.

Based on the nature of the chief effluent carried, the samples taken from the ditch receiving effluents from pipes *J* and *H* are spoken of in this paper as pulp-mill effluents, those taken from the ditch receiving the effluents from pipes *A*, *B*, *C*, and *D*, as paper-mill effluents, and those taken from the ditch draining the sludge pond as sludge-pond effluent.

PHYSIOLOGICAL EFFECT OF RIVER WATER CONTAINING PULP- AND PAPER-MILL WASTES

The first problem encountered in a study of the effect of industrial wastes on aquatic organisms is the determination of the concentration of the pollutant in the water. This presents little difficulty in cases of metallic salts, acids, or other substances which can be detected and quantitatively determined by available chemical methods. In the case of pulp-mill effluents, consisting of a complex mixture of various organic compounds and mineral salts, such a direct approach is impossible because of the absence of specific reactions. The situation is further complicated by the fact that the chemical nature of the toxic component or components of the sulfate-mill effluents is not known.[6]

In search of some method, it was first thought possible to apply the Folin-Dennis reaction for phenol, as many phenolic compounds in sulfate pulp-mill waste produce a blue color when allowed to react with this reagent. Many tests were made on samples of water collected at various distances from the pulp-mill in the York River, at many locations in the Piankatank River, and from a number of places throughout the general area of the lower Chesapeake Bay. The procedure used was that of Vorce (1925), who applied this test to water analysis. The results were, however, inconsistent and unreliable for an estimation of the concentration of sulfate-mill waste in the sea water because it was apparent, and confirmed by supplementary tests, that besides lignin and other components of pulp-mill waste, the waters of the river contain a number of other substances, not derived from the industrial waste, which give a blue color with the Folin-Dennis reagent.

Although it was impossible by chemical determination to obtain accurate measurements of the amount of pulp-mill effluents present in the York River, it was obvious that the upper river contained this material in considerable amounts. The presence of the physiologically active material of the effluents in the river in relatively high concentrations was demonstrated in two types of biological tests and observations on oysters. One of these showed the effects of river water of the upper York River on the rate of water filtration of oysters and the other the effect of this water on the time oysters remain open.

Frequently, pulp-mill effluents containing large amounts of black liquor were discharged into the Pamunkey River off the city of West Point. On the morning of the sampling, the river was brown with the effluent and a large area was covered with foam and froth. At this time two 5-gallon bottles of river water were taken at the bridge across the Pamunkey River just above its junction with the Mattaponi River to form the York.

After being brought to the laboratory, the sample was filtered through a double thickness of cheesecloth to remove the larger pieces of fiber. In order to avoid subjecting the oysters to sudden changes in salinity, the samples were adjusted to the approximate salinity of the laboratory supply of sea water by the addition of sea salts. These salts were obtained by evaporation of laboratory sea water after centrifuging with the Foerst highspeed centrifuge to remove the larger plankton forms, and drying the residue. The salinity of the sample was found to be 10.28 parts per thousand and the laboratory sea water 21.28 parts per thousand. Sea salt was added to the sample so that the salinity, when tested, was 21.94 parts per thousand. The difference between the sample and the laboratory sea water in which the oysters were acclimated was less than normal daily fluctuations in the salinity of the water at Yorktown.

The observations consisted in determining the rate of water filtration by the gills of normal oys-

[6] A nitrosolignin test, Pearl and Benson (1940), successfully used by Benson, Kobe, and Scott (1941) in determining the concentration of sulfite waste liquor in sea water, had not been published at the time the York River studies were made.

ters using the drop-counting method described by Galtsoff et al. (1935). Oysters were placed both in the laboratory supply of sea water and in the sea water collected in the upper York and adjusted to Yorktown salinity. The method, in general, consists of measuring the amount of water pumped by an oyster in a flowing salt water system. By means of an electric drop counter, the amount of water is recorded automatically on a kymograph drum. Because of the limited amount of test material, the solution was recirculated. In analyzing the kymograph records, the average number of drops per second was determined for each 10-second interval during the entire period of counting, which usually lasted from 2 to 2½ minutes. For convenience in plotting, the figures thus obtained were multiplied by 60 to represent the mean number of drops per minute. The results of these tests are presented in figure 44. The periods preceding and following the treatments may be considered as controls, indicating the rate of filtration in unpolluted river water.

The findings clearly show that, at times, the river water at West Point contained sufficient pulp- and paper-mill wastes to exert a very strong physiological action on oysters. When the normal oysters were exposed to this water containing large amounts of these wastes, they immediately changed their rate of pumping, the rate dropping to a very low level, or they stopped pumping completely. Even when this water was diluted 10 times with unpolluted sea water, there was a marked reduction in the ciliary activity of the oysters exposed to it. The effects were not permanent and the oysters filtered water at their normal rate once the test material was removed.

As the live oyster must keep the shell open a considerable part of the time, any agent in the water that would reduce the hours per day open must be regarded as injurious to the oyster, for it would interfere with its feeding and respiration. For a study of the possible effect of pulp-mill effluents in the water in the upper York River on oysters, observations were made of the time oysters in the river remained open at West Point below the pulp mill, at Allmondsville which is about half way between West Point and Yorktown, and at Yorktown.

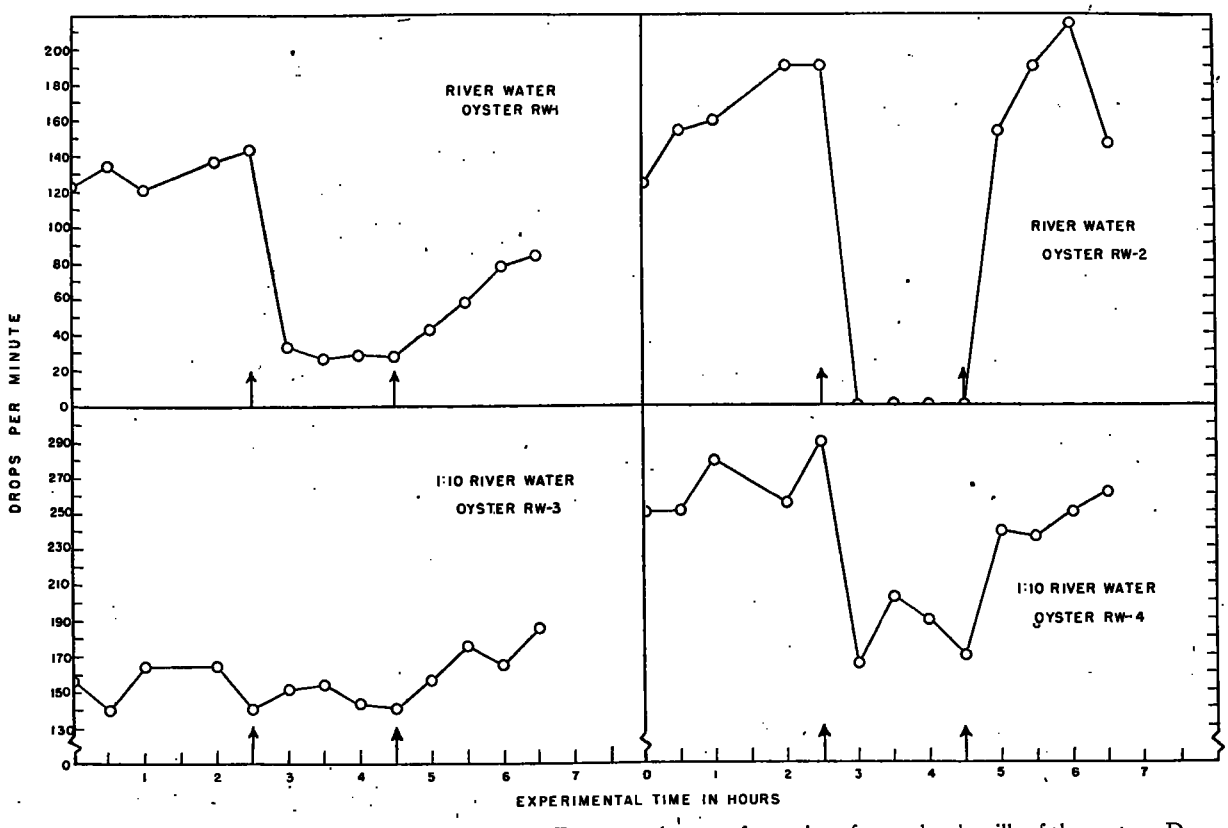

FIGURE 44.—Effect of river water polluted with pulp-mill effluents on the rate of pumping of water by the gills of the oyster. Drop-counting method. Samples of water used in this experiment were collected at the Pamunkey River Bridge.

TABLE 44.—*Time oysters remain open at various locations in the York River*

Location	Dates of observation (inclusive)	Days observed	Water temperature range, C°	Salinity range parts per thousand	Mean hours per day open
West Point	Aug. 15–Sept. 13, 1936	30	24–28	10.3–15.9	14.3
	Oct. 14–Nov. 24, 1936	42	10.21	11.6–16.5	21.8
	Apr. 2–28, 1937	28	11–18	0.2– 7.5	12.3
	Aug. 20–Oct. 17, 1937	59	[1] 23–30	[1] 4.4–12.6	16.8
	Nov. 6–29, 1937	24	8–14	0.6– 7.2	11.0
Allmondsville	Aug. 13–26, 1937	12	26–28	14.7–17.9	21.3
	Aug. 21–30, 1937	10	26–28	15.9–17.9	21.5
	Sept. 16–Oct. 5, 1937	17	19–22	13.9–17.1	20.8
	Sept. 25–Oct. 5, 1937	11	19–21	15.1–17.1	21.8
Yorktown	Aug. 18–Sept. 9, 1936	19	25–28	21.3–23.2	20.3
	May 10–26, 1937	17	18–23	12.0–16.2	21.7
	Aug. 21–Sept. 10, 1937	21	26–27	18.5–23.0	21.1

[1] Represents observations made Aug. 20 to Sept. 16. Temperature and salinity were not observed from Sept. 17 to Oct. 17.

For these observations oysters were selected from the locality near the place of testing so as to avoid changes in their environmental conditions during the period of observation. They were mounted on their left valve in blocks of a mixture of plaster of paris and cement and a small hook was attached to the movable right valve. The blocks with the oyster partially imbedded were securely fastened to a small wooden platform to which was attached a wooden upright lashed to the end of a section of pipe in such a way that the oyster to be observed was just below the pipe opening and the pipe lowered in position in the water. A light chain, attached to the hook on the right valve of the oyster, was led through the pipe and attached at the upper end to a recording lever, counterbalanced to compensate for the weight of the chain, and to give a slight pull on the oyster, a pull just sufficient to allow the lever to fall as the oyster opened. In most instances the lever ended in a writing tip in contact with the smoked paper of a kymograph drum, but at Allmondsville the lever was connected to a motion recorder marking with ink on a revolving paper clock-face. A similar arrangement for recording the shell movements of clams is fully described and pictured by Loosanoff (1939). At all the locations, the apparatus was placed in adequate housing to protect it from the weather.

Recordings were made of the activities of 5 oysters at West Point, 4 oysters at Allmondsville, and 3 oysters at Yorktown for periods ranging from 10 to 59 days from August 1936 to December 1937. Conditions of temperature and salinity during observation were recorded. The results of the observations on the time the oysters remained open are summarized in table 44.

In all cases but one, the oysters in the river at West point were open considerably less time than oysters at Allmondsville and Yorktown. Even in the instance when the hours open were not reduced, the kymograph tracings of the behavior of the adductor muscle showed a physiological reaction to the presence of pulp-mill effluent in the river. It consisted in a series of repeated and rapid shell movements followed by periods of extended closure. This abnormal behavior took place at those times when the observer reported marked discoloration of the water with effluent. Similar response of oysters to the presence of pulp-mill effluent in sea water was often observed in the laboratory (figs. 45–46), and was used in certain work as a bioassay method to determine the presence of the physiologically active material on pulp-mill effluents in test samples. A more complete description of the nature of the shell activity of oysters exposed to pulp-mill effluent in sea water is described later in connection with certain laboratory experiments.

From the foregoing it definitely can be stated that the river water of the upper York River contained the physiologically active material of the pulp-mill effluent in sufficient amount to produce an effect on oysters. The laboratory experiments described in the following sections serve to explain more fully the nature of the physiological effects of mill effluents in sea water at various concentrations under controlled conditions.

EFFECT OF PULP- AND PAPER-MILL EFFLUENTS ADDED TO SEA WATER ON THE TIME THAT OYSTERS REMAIN OPEN

The measurement of the hours per day that oysters remain open under controlled conditions gives an easy physiological method of determining the injuriousness of materials in the surrounding water, as the oyster normally keeps the shell open a considerable part of the time for feeding and respiration. Any agent reducing the hours open would eventually injure the oyster.

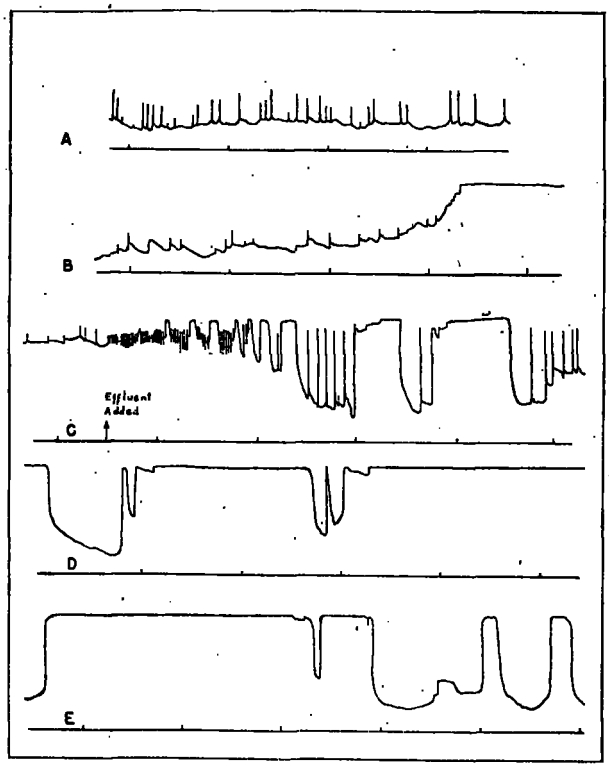

FIGURE 45.—Kymograph records showing the shell movement of normal oysters and an oyster exposed to pulp-mill effluent at a concentration of 1:10. The base line is marked in 1-hour intervals. A and B demonstrate normal activity of oysters in sea water. C shows the immediate response to the addition of pulp-mill effluent, which is followed by extended periods of shell closure. D and E present tracings showing continued shell closure with brief periods in which the oyster is open and a weakening of the adductor muscle. The writing pen is in the uppermost position when shells are closed.

The oysters employed for these tests were obtained from the lower York River. They were from 3 to 4 years old and in good condition. Preparatory to the experiments, they were brought into the laboratory and held for several days for acclimatization in tanks of running sea water.

The equipment used for the observations of the shell movement was essentially similar to that employed by Hopkins et al. (1931). The oysters were fastened to small cement blocks by their left valves. Light threads, attached to their right valves, were connected to levers which recorded the opening and closing of the shells on a slow motion kymograph. The oysters were placed in chambers receiving sea water, or a mixture of sea water and test material, running in from mixing chambers having a series of baffle plates. Test solution was added to a mixing chamber through a siphon tube connected to a container floating in the constant-level sea water supply. In this way the uniform rate of delivery of the solution was maintained. By controlling the rates of flow of sea water and of test solution supplied to the mixing chambers, it was possible to adjust the dilution of the material in the floating chamber so that the desired concentration would reach the oysters. In each test one oyster, used as a control, was kept in a chamber receiving unpolluted laboratory sea water delivered at the same rate as the water containing the known concentration of pollutant was delivered to two experimental oysters kept in an adjoining chamber. Thus, during each test, the control oyster was kept in identical conditions of temperature, salinity, and rate of flow as the two experimental specimens.

The kymograph tracings of shell movements of

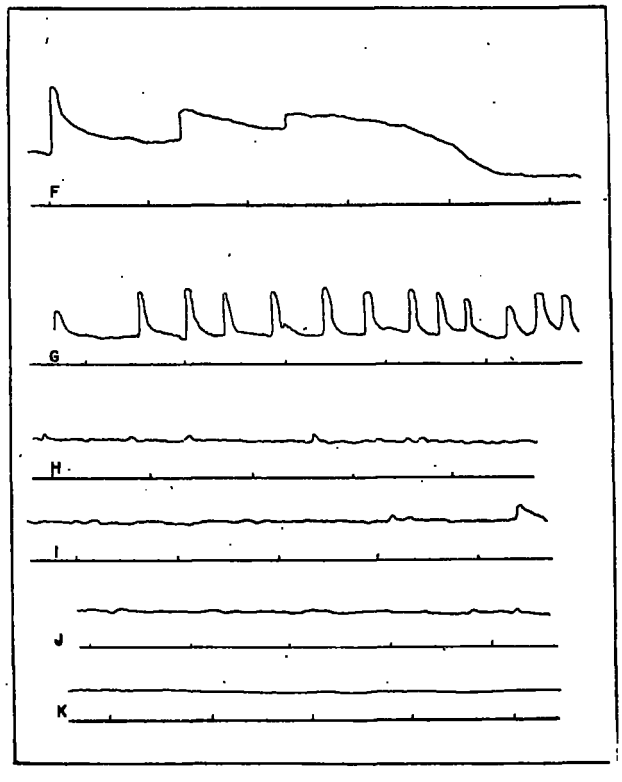

FIGURE 46.—Kymograph records showing the effects of prolonged exposure to pulp-mill effluent on the shell movement of an oyster. The tracings represent later periods in continuation of figure 45. F and G show the weakening of the adductor muscle with the oyster unable to hold the shell closed. H, I, and J give the record of the gaping of the shell with feeble attempts of the oyster to close the valves. K represents the final gaping of the shell with the death of the oyster. The writing pen is in the uppermost position when shells are closed.

the oysters were marked off into hours and analyzed as to the number of hours during each day the oysters were open. The duration of the experiments varied from 6 to 30 days during which shell movements were recorded continuously. Because each of the tests required many days, the experiments were made during the entire year at different ranges of temperature and salinity. The temperature of the solution in which the oysters were immersed was observed and recorded every morning and night. The salinity of the laboratory sea water was measured daily.

In analyzing the tracings of shell movement of the oysters, one must bear in mind that strong poisons frequently produce complete paralysis of the adductor muscle which results in the cessation of movements and gaping of the valves. Thus the number of hours per day the oyster remains open can be considered as an index of a normal behavior only if the curve of shell movement remains normal. Figures 45 and 46 representing normal behavior and the shell movements of an oyster affected by toxic substance illustrate this point. One can notice in the experiments with high concentrations of effluent (1:10), that after several days of treatment, the adductor muscle of the oyster became paralyzed and the shells remained completely open. The muscular contraction of these oysters were similar to those described by Hopkins et al. (1931) in his work on the effect of sulfite liquor on *Ostrea lurida*. In analyzing the data, the records that showed paralysis of the adductor muscle were not taken into consideration for determining the time the oysters remained open. The tests are summarized in table 47 which gives in a condensed form the conditions of each experiment and presents the results as the means of the number of hours per day the oyster remained open. The ranges of temperature and

TABLE 45.—*Effect of pulp-mill effluent on the time the oysters remain open*

Concentration of effluent	Oyster No.	Hours per day open		Dates of test (inclusive)	Water temperature range °C.	Salinity range parts per thousand	Eufflent No.	Specific gravity at 17.5° C.	Date collected
		Control	Experimental						
1 : 10	15-1	21.7	2.3	Nov. 6 to 12, 1936	12.5 to 17.1	23.32 to 22.74	6	1.0012	Sept. 8, 1936.
	15-2	21.7	7.8						
1 : 100	CB-5	22.3	8.0	May 11 to 17, 1936	15.4 to 23.6	13.17 to 16.08	3	1.0029	May 11, 1936.
	CB-6	22.3	9.0						
	CB-1	22.4	8.6						
	CB-2	22.4	12.8						
1 : 200	1-1	23.1	14.8	May 25 to 30, 1936	16.4 to 23.8	14.81 to 16.20			
	1-2	23.1	10.5						
	1-3	21.9	11.2						
	1-4	21.9	14.8						
	8-3	19.2	14.2	July 30 to Aug. 6, 1936	20.5 to 27.1	20.43 to 21.62	4	1.0021	June 14, 1936.
	8-4	19.2	15.3						
1 : 400	5-1	21.3	10.8	July 5 to 12, 1936	24.1 to 28.2	19.27 to 20.10	3	1.0029	May 11, 1936.
	5-2	21.3	17.4						
	5-4	20.5	15.9						
	5-5	20.5	14.9						
	7-1	20.0	14.1	July 16 to 25, 1936	25.3 to 27.2	19.72 to 20.68	4	1.0021	June 14, 1936.
	7-2	20.0	12.4						
	7-3	24.0	14.4						
	7-4	24.0	10.0						
1 : 1,000	2-1	21.3	9.8	May 25 to 30, 1936	16.4 to 23.8	14.81 to 16.20	3	1.0029	May 11, 1936.
	2-2	21.3	10.7						
	2-3	21.2	11.4						
	2-4	21-2	14.0						
	12-1	21.2	22.2	Oct. 19 to 27, 1936	17.3 to 20.7	22.83 to 23.57	6	1.0012	Sept. 8, 1936.
	12-2	21.2	17.5						
	12-3	21.3	13.0						
	12-4	21.3	15.7						
	18-1	20.4	10.5	Mar. 10 to 19, 1937	3.8 to 10.6	16.20 to 17.29	11	1.0039	Feb. 25, 1937.
	18-2	20.4	9.2						
	104	20.7	14.6	June 15 to 27, 1938			51	1.0014	June 13, 1938.
1 : 2,000	6-1	18.7	16.4	June 16 to 25, 1936	25.3 to 27.2	19.72 to 20.68	4	1.0021	June 14, 1936.
	6-2	18.7	19.1						
	6-3	18.8	17.1						
	6-4	18.8	18.8						
1 : 4,000	4-1	21.9	22.3	June 7 to 17, 1936	21.2 to 25.2	17.41 to 17.90	3	1.0029	May 11, 1936.
	4-2	21.9	21.7						
	4-3	22.7	22.3						
	4-4	22.7	15.8						
1 : 5,000	14-1	21.7	21.0	Nov. 7 to 27, 1936	6.3 to 16.1	21.00 to 23.75	6	1.0012	Sept. 8, 1936.
	14-2	21.7	22.7						
	19-1	21.3	19.1	Mar. 12 to 26, 1937	4.2 to 11.1	15.37 to 17.77	11	1.0039	Feb. 25, 1937.
	19-2	21.3	13.1						
	25-1	22.4	19.7	Apr. 26 to May 5, 1937	12.6 to 16.2	15.46 to 18.57	17	1.0053	Apr. 20, 1937.
	25-2	22.4	19.8						
1 : 10,000	3-1	22.1	22.0	June 2 to 29, 1936	19.4 to 27.0	16.09 to 19.94	3	1.0029	May 11, 1936.
	3-2	22.1	22.8						
	17-1	20.1	18.1	Mar. 12 to Apr. 11, 1937	4.2 to 13.3	15.37 to 17.90	11	1.0039	Feb. 25, 1937
	17-2	20.1	20.5						

salinity are written in the order of their occurrence to indicate the trend of the change experienced during the tests.

Physiological factors controlling the spontaneous muscular movements of the oysters are not well understood. It is known, however, that under normal conditions the oyster has a tendency to keep its shell open for very long periods of time, frequently exceeding 24 hours (Galtsoff 1928).

A summary of these data referring to the conditions under which each set of observations were conducted, as well as the nature of the test effluent, are shown in table 45. The observations were made using samples of mill effluents flowing into the river from the pulping process (sewers *J* and *H*), from the paper mill (sewer *A*), and from the sludge pond. The specific gravity and the color of the effluents were noted immediately upon collecting and the sample was stored in 5-gallon bottles which were well-corked and kept in the laboratory room.

Records of shell movement were obtained for 74 oysters. Of these, 49 oysters were treated with various concentrations of the mill effluents and 25 were used as controls. The results of all the experiments are given in figures 47 to 50 which show the hours per day that each oyster was open during the periods of observation.

The effectiveness of the various samples of effluent,

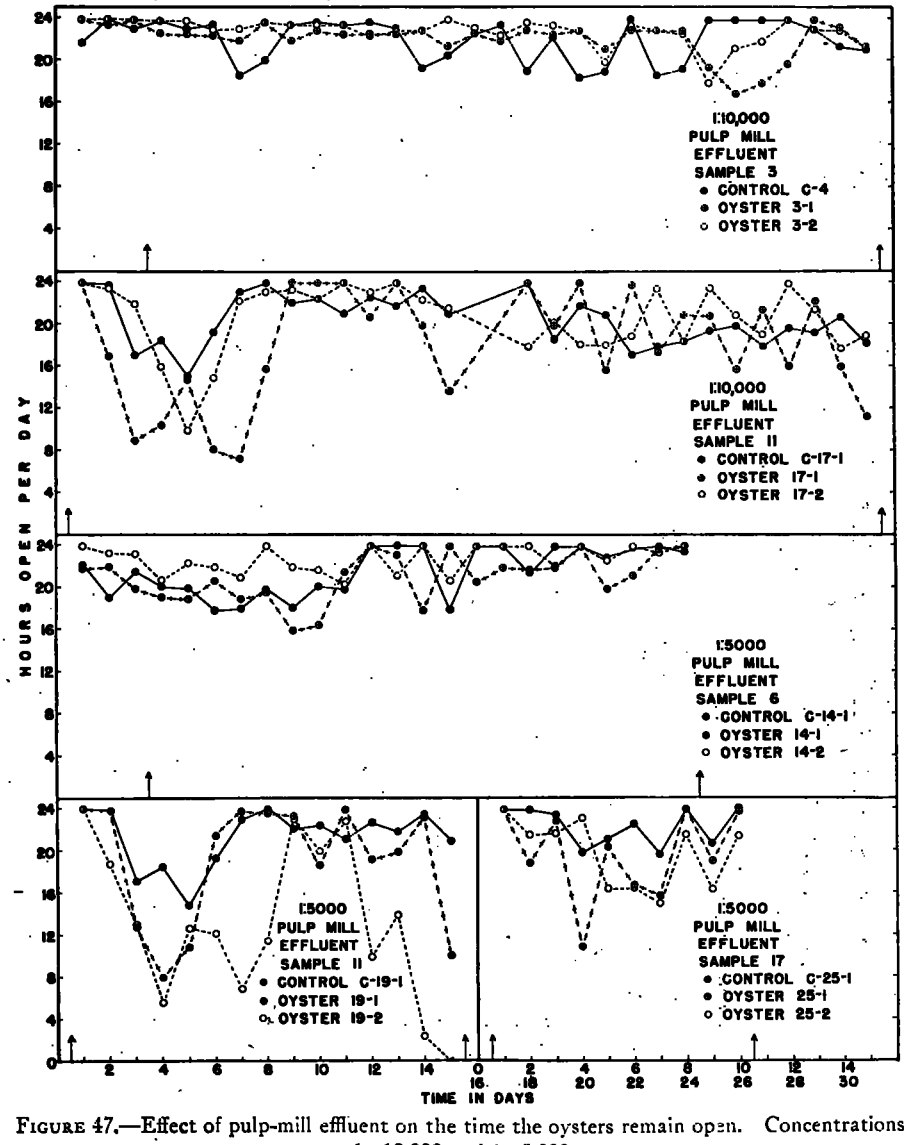

FIGURE 47.—Effect of pulp-mill effluent on the time the oysters remain open. Concentrations: 1 : 10,000 and 1 : 5,000.

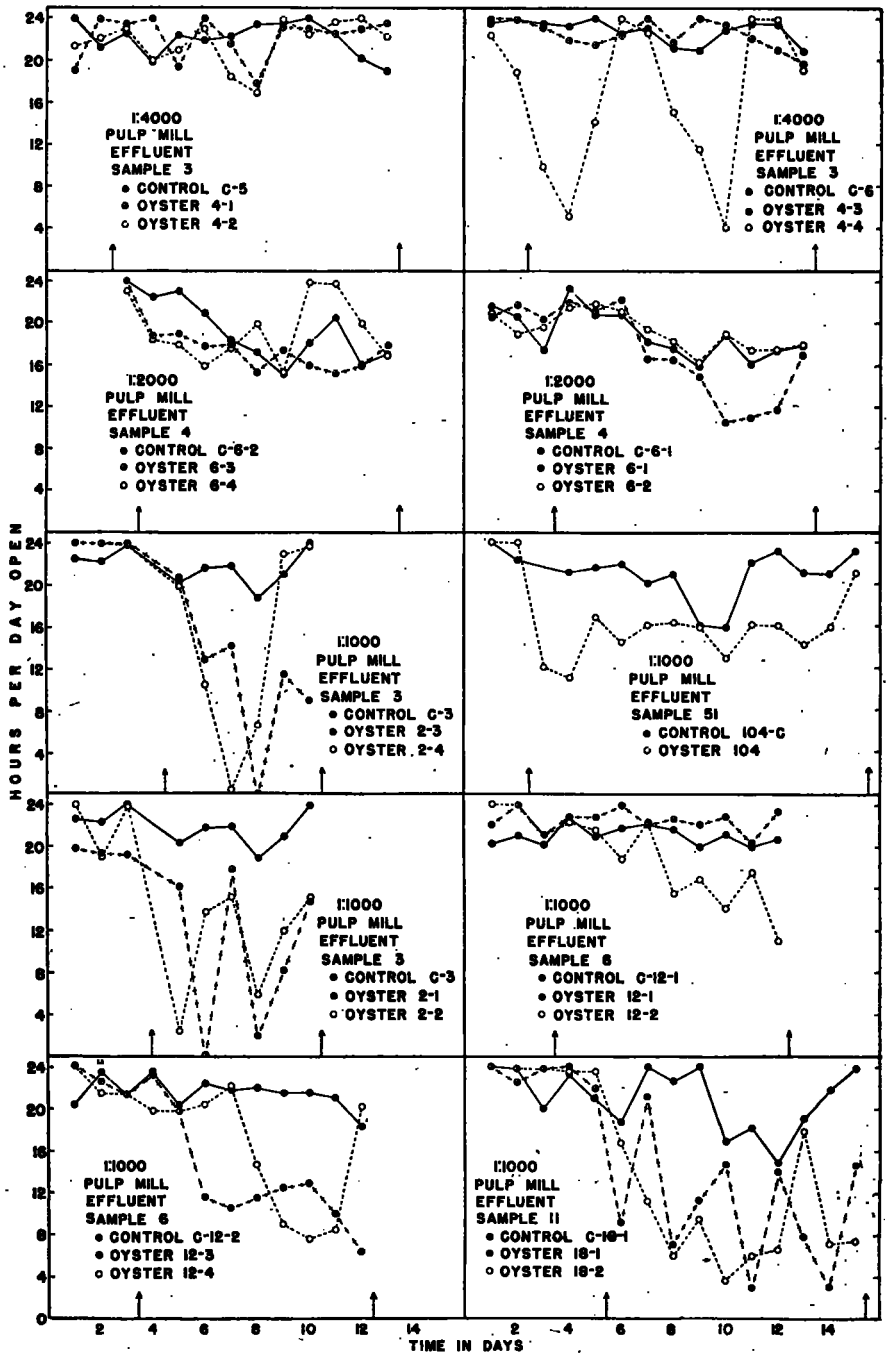

FIGURE 48.—Effect of pulp-mill effluent on the time the oysters remain open. Concentrations: 1 : 4,000, 1 : 2,000, and 1 : 1,000.

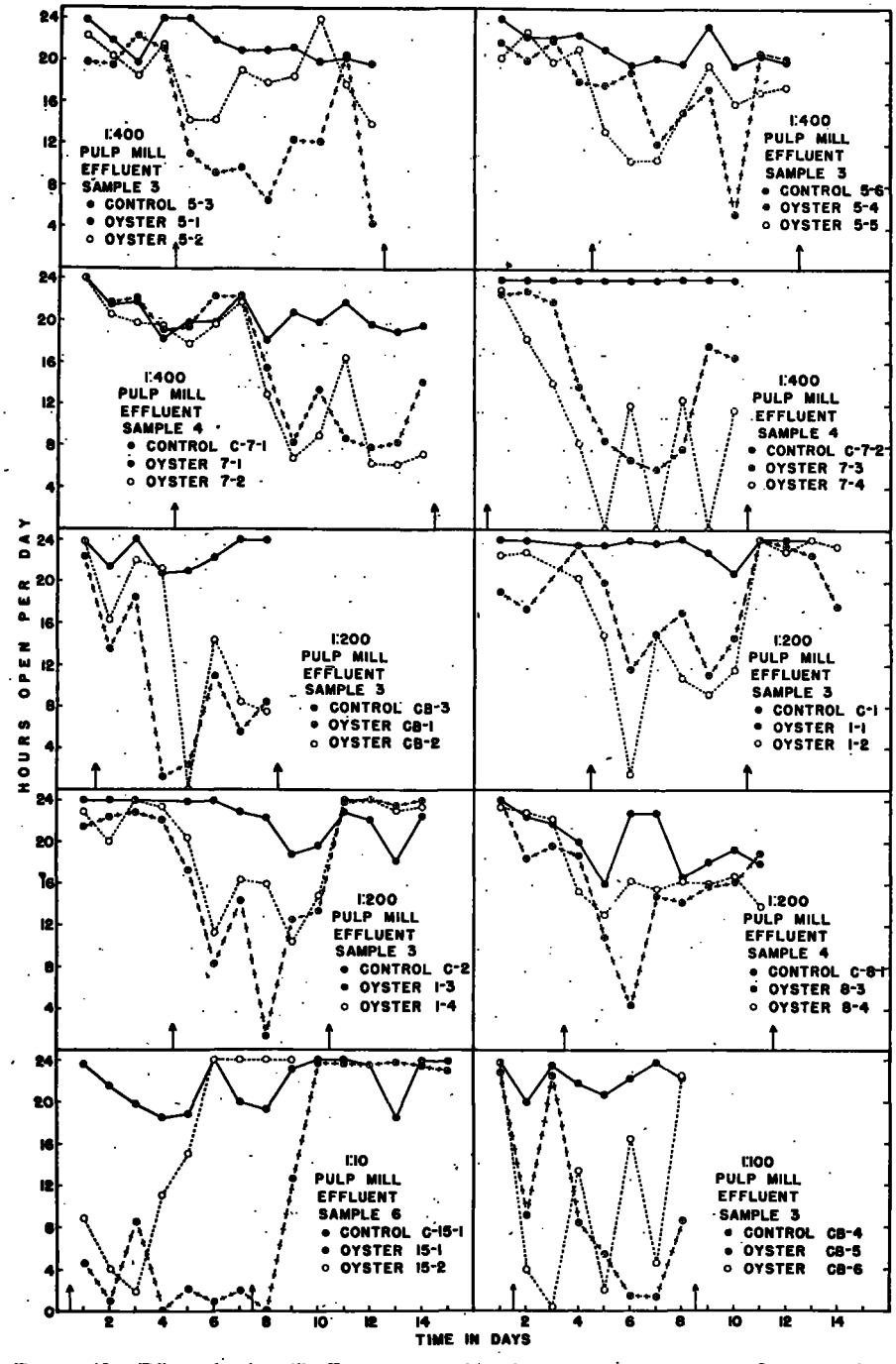

FIGURE 49.—Effect of pulp-mill effluent on the time the oysters remain open. Concentrations: 1 : 400, 1 : 200, 1 : 100, and 1 : 10.

collected at different times from the same sewer outlet, did not remain constant but was subject to change, associated with variations in the degree of dilution of the effluent, and changes in its character. The latter depended on conditions within the mill and also were associated with different stages of the manufacturing process. As these changes occurred suddenly and frequently, the time of flow of an effluent having a particular specific gravity, color, and other characteristic was of brief duration. For this reason the material used for testing consisted always of composite samples of the effluent collected at 15-minute intervals over a period of 5 hours.

Experiments reported later (pp. 159–163), showed changes in the physiological effectiveness of the effluents after storage and oxidation and after varied forms of treatment. There is no doubt, therefore, that the effectiveness of the effluent used in the experiments on the shell movements of oysters varied depending on its specific gravity, chemical composition, and age. Because the chemical nature of the physiologically active component of the effluent was unknown, it was decided not to adjust the effluent to an arbitrary specific gravity by evaporation. Such an adjustment, it was thought, might have produced changes in the effectiveness which would invalidate the tests. The various concentrations used in the experiments were prepared from the composite samples of effluent regardless of their specific gravity. There is no doubt that fluctuations in the composition of the effluent to a certain extent were responsible for the variability in the results, especially in the experiments in which low concentrations of the effluent were used. It is our opinion, however, that despite this variability, the experiments clearly show that the presence of the effluent in the river water causes the reduction in the number of hours the oyster remains open.

Laboratory experience shows, however, that in a sample of an oyster population several oysters are always present which, when placed in water and adjusted to the new environment, remain open for a much shorter period of time than the others. Because of this situation single tests are of little significance. It is necessary to have a large number of observations and make comparison between the means computed for each series of tests. A glance through table 45 shows that the daily mean number of hours the control oyster remained open under different temperature and salinity ranges varied from 18.7 to 24.0. Analyses of individual records made for each day separately shows that occasionally some were open only from 12 to 15 hours per day but, in the majority of cases, the oysters stayed open from 21 to 24 hours a day. It can be noticed easily that the addition of pulp-mill effluent reduces the number of hours open as the concentration of the effluent is increased. This negative correlation is apparent from examination of table 46 showing the frequency distribution of the number of hours open in various concentrations. Vertical columns give the total number of days the oysters were open for the specified number of hours indicated in the first column. The totals given at the bottom of the table cannot be used for direct comparison because the number of days for which the muscular activity was recorded in the controls and for the two lowest concentrations (1:10,000 and 1:5,000) were much greater than for other dilutions of the effluent. Experiments with the lower concentrations were continued for longer periods of time with the expectation that an adverse effect of a pollutant may be cumulative and would become apparent only after a prolonged exposure. On the other hand, in the tests with higher concentrations (1:100 and 1:10), pronounced toxic action was noticeable in a few days. In several

TABLE 46.—*Frequency distribution of "hours open" in various concentrations of pollutant*

Figures in the body of the table indicate the number of days during which oysters remained open for a number of hours shown in the first column. Total number of oysters used: in controls (0 concentration)—24; in tests—49. Duration of the experiments from 6 to 30 days; for details see table 45]

Hours open	Concentrations of pollutant in sea water									
	0	1/10,000	1/5,000	1/4,000	1/2,000	1/1,000	1/400	1/200	1/100	1/10
21–24	145	80	51	31	8	15	4	4	2	
18–21	94	16	18	5	9	10	9	5		
15–18	19	11	9	3	19	9	12	20	1	
12–15	3	2	5	1	1	11	10	17	1	
9–12		3	5	2	3	14	6	11	1	1
6–9		3	2			9	9	7	2	2
3–6			1	2		4	2	2	3	2
0–3			2			7		6	4	6
Total	261	115	93	44	40	79	52	72	14	11

cases, oysters used in the latter experiments were dead or dying by the end of the experiment. The experiments with the dilutions of pulp-mill effluent thought likely to occur in the York River were performed on a greater number of oysters and for longer periods of time than those with stronger concentrations.

Summary of observations of the time the oysters were open in various concentrations of the effluent are given in figures 47 to 49, while temperature and salinity data, referring to these experiments, together with the specific gravity of the samples of pulp-mill effluent can be found in table 45. In the concentration of 1 : 10,000 no significant reduction in the hours open was noticed by the end of the test lasting 30 days (fig. 47) and the shell movements of the oysters remained normal. In oysters 3–1 and 3–2, slight reduction in hours open occurred on the twenty-fifth day and continued for 4 days. It was, however, of temporary nature. We may infer from these data that a continuous exposure to the concentration 1 : 10,000 lasting for one month produces no noticeable effect in the number of hours the oysters remain open. It is, of course, possible that an adverse effect may become apparent later, but because of the lack of space in the temporary laboratory at Yorktown, it was impractical to prolong a single experiment beyond the 31-day period.

Of the six oysters used in the tests with the concentration of 1 : 5,000, two oysters exposed for 25 days were not affected by the pollutant; in three oysters the mean number of hours open during an 11-day period was slightly reduced, namely from 21.7 and 21.3 in the controls to 19.1 and 19.8 in the experiments, and one oyster was open only 13.1 hours as compared with 21.3 hours for the control. It is reasonable to assume that the toxicity of the effluent, sample 6, used in treating the first pair of oysters was less than that of samples 11 and 17 used in the other tests, because the specific gravity of sample 6 was only 1.0012 as compared with 1.0039 and 1.0053 of samples 11 and 17, respectively.

With the increase of concentration to 1 : 1,000 (fig. 48), the effect of the effluent is apparent within 1 or 2 days after the beginning of the test and becomes more and more pronounced as the concentration increases.

Variability in the results of the test can be attributed chiefly to the changes in the toxicity due to the dilution of the effluent by wash water and its degree of oxidation. Despite these conditions, the general tendency of the oyster to reduce the number of hours open as the concentration increases is quite clear.

High concentrations varying from 1 : 400 to 1 : 10 have a more pronounced effect as can be easily seen from the examination of figure 49. In the case of the latter concentration (see lower left of figure) rapid increase in the hours open recorded after the fourth day of exposure was due to the paralysis of the adductor muscle.

Relationship between the number of hours the oysters are closed and the concentration of the effluent can be seen clearly by plotting the mean number of hours the oysters stay closed against the log of concentration of the effluent. In making this plotting, the mean values were computed for each concentration used in the experiments listed in table 45. The values of means with their standard deviation and standard errors are given in table 47. For convenience in plotting, the concentrations are expressed in parts per 10 liters. The line was fitted by inspection. As can be seen from figure 50, there is a definite relation between the number of hours closed and log-concentration. As the plot of (x, log y) approximates a straight line, the set of the experimental data may be represented by an exponential equation of the form of $y=ae^{bx}$. Constants a and b, determined by the method of averages, are as follows: $a=0.2814$ and $b=0.4234$. The numerical value of e is, of course, 2.718. Thus, the equation representing the mean number of hours the York River oysters remained closed in a given concentration of the effluent can be written in the following form:

$$x=\frac{\log y+0.5504}{0.1839}$$

TABLE 47.—*Mean values of hours open (M) and closed (M^1) in various concentrations of pulp-mill effluent*

[N=number of oysters under observations, N^1=number of oyster-days, x=number of hours closed computed from equation $y=ae^{bx}$ when y=is concentration in parts per 10 liters, a=0.2814, b=0.4234, Δ=difference between the observed and computed values, σ=standard deviation of hours open, S.E.=standard error]

Concentration in parts per 10 liters	M	σ	S.E. ±	M^1	N	N^1	x	Δ
1,000	5	------	--------	19.0	2	11	19.3	−0.3
100	8.5	------	--------	15.5	2	14	13.9	+1.6
50	12.8	2.40	0.85	11.2	8	72	12.2	−1.0
25	13.7	2.52	0.89	10.3	8	52	10.6	+0.3
10	13.5	3.89	1.17	10.5	11	79	9.0	+1.5
5	17.9	1.29	0.65	6.1	4	40	6.8	−.07
2.5	20.5	3.15	1.57	3.5	4	44	5.2	−1.7
2.0	19.2	1.63	0.67	4.8	6	93	4.6	+0.2
1.0	20.9	2.06	1.03	3.1	4	115	3.0	+0.1
0	21.3	1.29	0.26	2.7	25	261	------	------

TABLE 48.—*Effects of paper-mill and of sludge-pond effluent on the time the oysters remain open*

Concentration of effluent	Oyster No.	Hours per day open		Dates of test (inclusive)	Water temperature range ° C.	Salinity range parts per thousand	Effluent No.	Specific quantity at 17.5° C.	Date collected
		Control	Experimental						
Paper-mill effluent									
1 : 200	8-1	19.9	12.2	July 29 to Aug. 6, 1936	20.5 to 27.1	20.43 to 21.62	5A		July 14, 1936
	8-2	19.9	14.7						
1 : 500	22-1	27.1	22.2	Mar. 24 to Apr. 3, 1937	6.5 to 11.1	9.85 to 13.73	13		Mar. 12, 1937
	22-2	22.1	22.2	June 15 to 27 1937			52	1.0013	June 3, 1937
	103	20.8	19.4						
1 : 1,000	20-1	22.1	21.7	Mar. 10 to 19, 1937	5.8 to 9.8	16.20 to 17.29	12	1.0018	Feb. 25, 1937
	20-2	22.1	21.7						
	101	22.1	22.3	June 3 to 10, 1938			49	1.0049	May 31, 1938
Sludge-pond effluent									
1 : 500	105	17.2	18.3	June 18 to 22, 1938			53		June 13, 1938

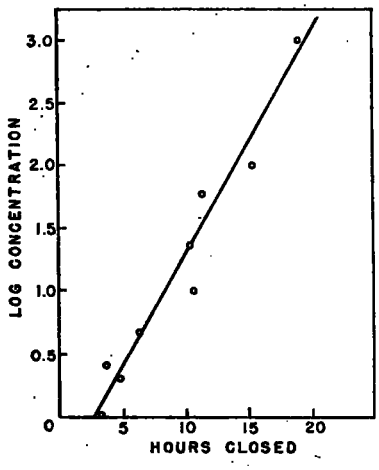

FIGURE 50.—Relation between the hours the oysters are closed and log concentration of pulp-mill effluent discharged into York River.

The reliability of the equation can be judged by comparing the observed and the computed value of x in table 47.

Physico-chemical basis of the equation cannot be evaluated at present because of the lack of understanding of the chemical nature of the physiologically active component of the pulp-mill effluent and of its effect on the neuromuscular system of the oyster. The type of the exponential equation suggests, however, that probably the mass law is involved and the reactions responsible for the prolonged contraction of the adductor muscle depend on the effective concentration of the reacting materials.

Physiological effect of the pulp-mill effluent is shown also on the type of muscular activity of the oysters. There was a marked change in the shell movements of oysters subjected to solutions containing pulp-mill wastes in concentrations of 1 : 1,000 or stronger. Irritating effect of the effluent was characterized by rapid and frequent shell closures at the time the effluent was added. These changes are clearly noticeable on the kymograph records reproduced in figure 45C.

The periods of high activity were followed by long periods in which the oysters remained tightly closed. In the stronger concentrations, the periods of closure became less frequent and as the adductor muscle weakened, the oysters were unable to hold the valves together for any length of time. In a concentration of 1:10 the amplitude of the movement of the adductor muscle, during the brief periods of attempts to close the shell, became less and less, and finally the shell remained open and the oyster died (fig. 46J and K). Under the conditions of the experiment, death of the oysters occurred only in concentrations in 1:10.

In comparison with the pulp-mill waste, the paper-mill effluent is much less toxic. Tests performed with the latter show that its effect becomes noticeable only in the concentration of 1:200 (table 48). Only one experiment was performed with the effluent from the sludge pond. No effect was observed in the dilution of sludge water at 1 : 500 (fig. 51).

EFFECT OF PULP- AND PAPER-MILL EFFLUENTS ON THE WATER FILTRATION OF OYSTERS

Pumping of water by the oyster for feeding and respiration is dependent on the combined activities of the ciliated epithelium of the gills, the adductor muscle, and the mantle. The ciliated lining of the gills provides a mechanical force which drives the water through a system of water pores and tubes, whereas the contractions of the adductor muscle and the mantle control the flow of water by regulating the opening and closing of the mantle chamber

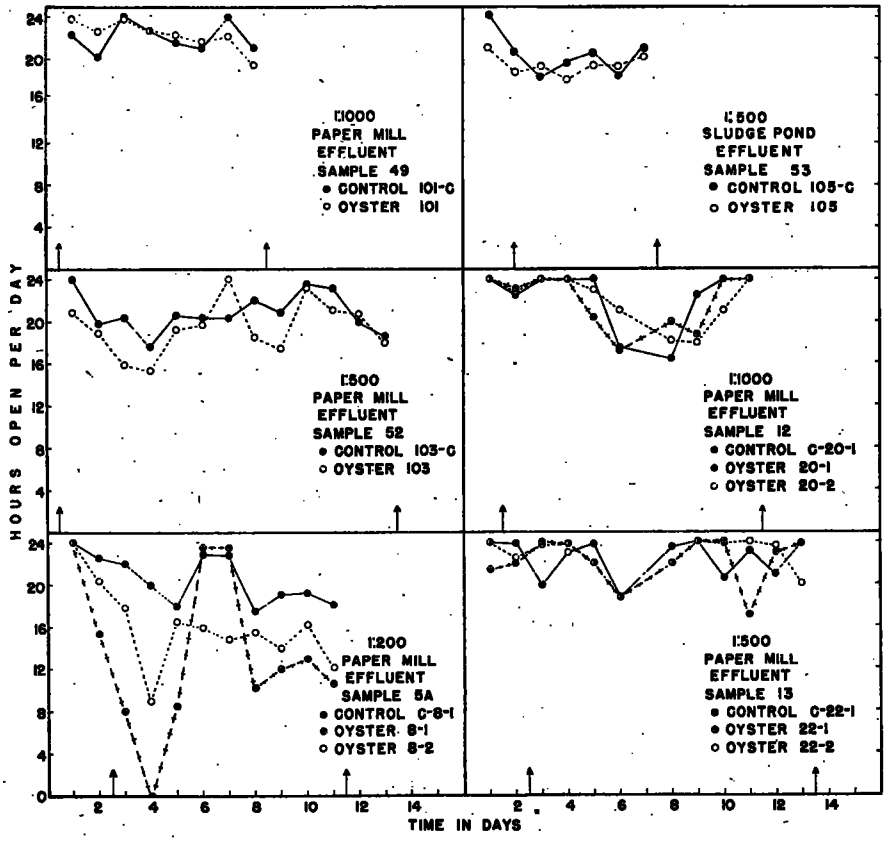

FIGURE 51.—Effect of paper-mill and sludge-pond effluents on the time the oysters remain open.

to provide for a greater or lesser access of the outside water to the gills. To obtain a clear understanding of the functions of these organs in the presence of the pollutant, three sets of experiments were conducted.

The effect of various concentrations of the pulp-mill effluents on the ciliated epithelium of the gill was studied by using the two methods previously developed by Galtsoff (1928, 1935) generally known as the carmine-cone method and the drop-counting method. For a study of the effect of pollutants on the entire feeding mechanism of the oyster a combination of Nelson's apron method (Nelson 1936) and Galtsoff's constant-level tank (1928), employed in the drop-counting method, was used. In the apron method continuous records of the pumping of the water by the intact oyster were obtained for periods lasting from several days to about a fortnight.

Experiments Using the Carmine-Cone Method

Normal adult oysters, collected from the vicinity of the laboratory, usually from the lower York River, were employed. They were brought to the laboratory in lots of a half to 1 bushel as needed and stored in a tank of flowing laboratory sea water.

On the morning of testing, oysters were selected from the stock supply and the valves carefully pried ajar without injuring the adductor muscle and a small glass rod inserted. The valves were then wired to prevent any further opening. A small rubber tube was then inserted into the cloaca and the remaining space berween the valves on the excurrent side filled with wet cotton. After removing any air bubbles trapped in the valves and tube by means of a bulb pipette, the oyster was placed in an enamelware tray containing 8 liters of sea water. A stream of bubbles passing through a tube in the tray circulated the water. The rubber tube was then connected to one arm of a glass "⊥" tube onto which had been attached a glass tube marked with two marks 15 centimeters apart. The upright arm of the "⊥" tube was connected to a small thistle tube containing a light carmine suspension held in the tube by a Day's pinchcock clamp. By releasing a small amount of carmine by

slight pressure on the clamp, the suspension joining the water being pumped by the oyster formed a red cone, the tip of which was timed by a stop watch as it passed between the two marks.

After allowing the oyster time to recover from shock, the rate of pumping in plain sea water was determined, 10 readings in succession being averaged. Usually one investigator could test three oysters, two experimental and one control. After readings at half-hour intervals had shown the oyster to be pumping at a regular rate, the test solution was added from a pipette in an amount sufficient to bring the concentration to the desired strength. An electric stirrer was then turned on for 10 minutes. Using this technique two sets of experiments were performed. In the first series of tests, the concentration of the effluent was gradually increased and readings were made 15 minutes after each addition of effluent. In the second series, oysters were kept for several hours in a given concentration of effluent: during the first 2 hours readings were made every half hour, then at greater intervals.

In the tests which were conducted in the summer of 1936, oysters were subjected to gradually increasing concentrations of a composite sample of effluent taken from sewers *J* and *H*. The specific gravity of sample No. 3 was 1.00285. To eliminate variations of salinity and temperature in any one experiment, the tests were designed to be completed within a 24-hour period. In no experiment did the temperature vary more than 2° C. Moreover, there was no appreciable change in salinity in any experiments except in those where the concentration of effluent exceeded 30 parts per thousand and the sea water was noticeably diluted by the pollutant. The hydrogen-ion concentration was taken into consideration. Significant increase in pH varying from 0.3 to 0.4 occurred only when the concentration of the effluent reached 30 parts per thousand and above.

Each experiment was adequately controlled, i. e., control was observed simultaneously with two experimental oysters. The percentage of the depression was computed by considering as 100 percent the rate of flow of each test oyster before the addition of the effluent. The controls served as a check against any possible decrease in the rate of flow resulting from fatigue, changes in temperature, and other factors. Since there was no actual distinction in the controls between the periods before and during treatment, separation has to be made arbitrarily on a time basis. One hour prior to treatment, at least two series of readings were made at 30-minute intervals. A similar number of readings was made at the end of each test period which, on different occasions, varied from 5 to 26 hours. An inspection of the rates of flow of the controls showed that 12 out of 13 oysters increased their rate of pumping during the test period. This indicated that any depressive effect observed in the test oyster could not be attributed to the condition of the experiment and was due to the presence of pollutant. The pulp-mill effluent was added in gradually increasing amounts that resulted in the following concentrations: 5, 10, 20, 30, 40, and 50, parts per thousand. The results, computed as means of all the observations for a given concentration, are presented in figure 52. They show a definite relationship between the increase in the concentration of the pulp-mill effluent and its physiological effect on ciliated epithelium. Using the same technique, numerous tests were made in 1937 and 1938 with different samples of pulp-mill and paper-mill effluents. The results of some of these experiments, presented in figure 53, show considerable variation in the physiological effectiveness of various samples, a fact already noticed in other tests (pp. 137–140). If, however, the same sample of the pollutant was used to test

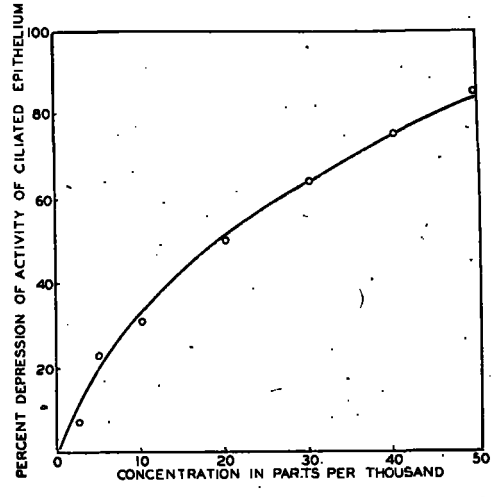

FIGURE 52.—Effect of increased concentration of pulp-mill effluent (sample 3, specific gravity 1.00285) in depressing the activity of the ciliated epithelium of the gill measured as a velocity of the cloacal current. Carmine-cone method. Each point represents mean of observations on nine oysters. Samples collected May 11, 1936. Tests performed between May 14 and 20, 1936.

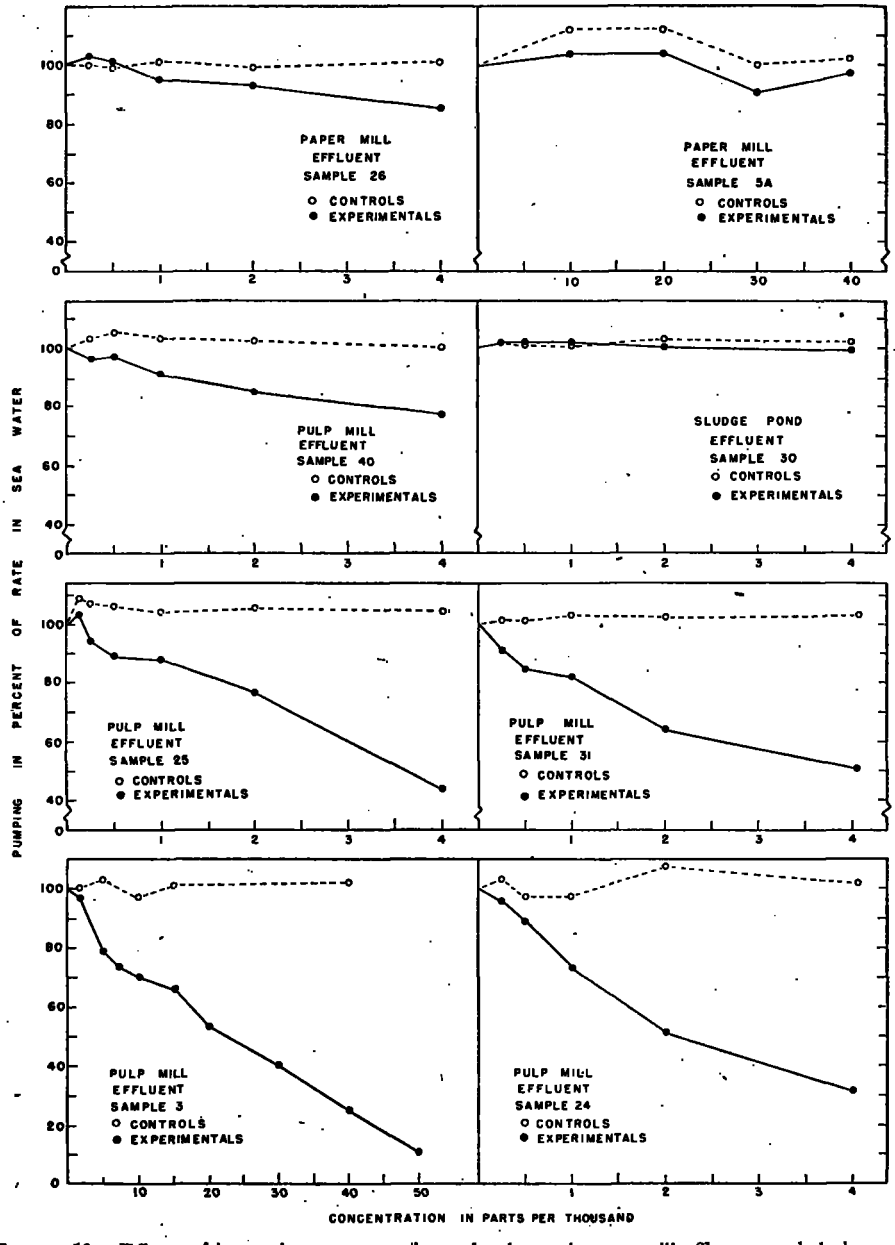

FIGURE 53.—Effects of increasing concentrations of pulp- and paper-mill effluents and sludge-pond effluent on the ciliary motion of the gill epithelium as measured by the carmine-cone method. Each point on the curves represents the average of five or more oysters. Exposure time was a half hour after the desired concentration was attained except for sample 3 in which a 15-minute exposure was used.

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its effectiveness in various concentrations, the relation between the degree of depression of the rate of pumping and concentration followed the same general trend shown in figure 52.

From the point of view of toxicological studies, the method in which the concentration of toxic material is being gradually built up is open to criticism because under this condition the response of the organism may result from prolonged exposure to low concentration of a physiologically active substance plus the additional effect of stronger concentrations. On the other hand, oysters located near the source of pollution are frequently subjected to gradually increasing concentrations of pulp-mill effluent, which is being discharged at a greatly variable rate. The laboratory tests to a certain extent reproduce these conditions.

The results of tests in which a given concentration of the effluent was kept constant are shown in figure 54 which summarizes the observations made with various samples of pulp- and paper-mill effluents. From the examination of the curves, it is apparent that physiologically active material, which depresses ciliary activity of the gills, is present in varying amounts in different samples. Thus, sample 5 was effective only in a relatively high concentration of 1:100, samples 3 and 6 were effective in dilution of 1:200, and the effect of samples 23 and 24 was very pronounced in rather low concentrations of 1:2,000 and even 1:4,000. Details of these and other

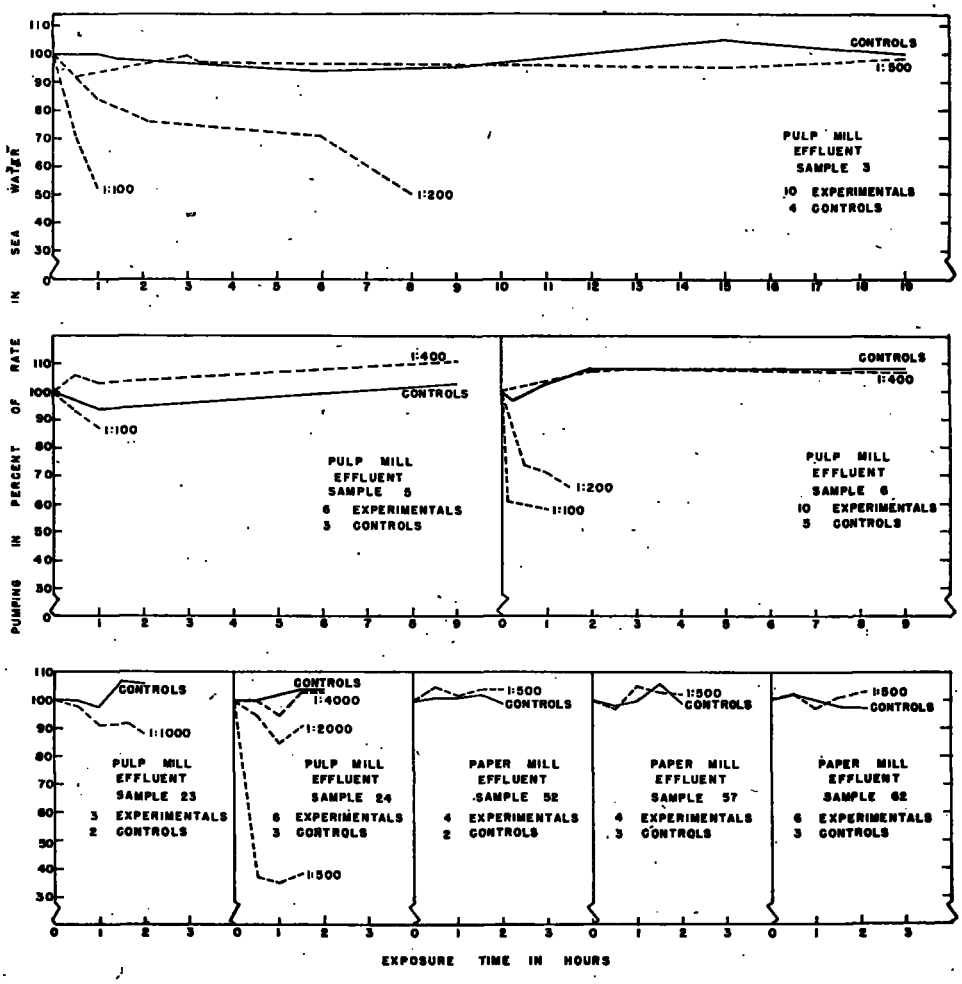

FIGURE 54.—Effects of exposure to various concentrations of pulp- and paper-mill effluents on the ciliary motion of the gill epithelium as measured by the carmine-cone method. The plotted points represent the averages for the number of oysters indicated in each block of the graph. During each test the concentration of effluent indicated on the graphs remained unchanged.

TABLE 49.—*Conditions of the experiments using the carmine-cone method with fixed concentrations of the pulp- and paper-mill effluents. (See figs. 54 and 56)*

Sample No.	Specific gravity at 17.5° C.	Concentration tested	Date of test	Salinity, parts per thousand	Water temperature range, ° C.	Sea water pH	Solution pH
Pulp-mill effluent							
3	1.0029	1:100	June 4, 1936	16.0	17.6 to 19.2	8.1	8.1
			July 27, 1936	17.7	27.6 to 27.9	7.8	----------
		1:200	May 28, 1936	14.1	24.9 to 19.6	7.9	7.9
			May 25, 1936	14.1	24.9 to 19.6	7.9	7.9
		1:500	May 26, 1936	15.3	21.3 to 23.0	7.9	7.9
5	1.0013	1:100	Aug. 21, 1936	21.3	27.7 to 28.8	7.8	----------
		1:400	Aug. 17, 1936	21.4	27.3 to 27.6	7.8	7.8
6	1.0016	1:100	Oct. 15, 1936	----------	21.5 to 21.9	----------	----------
		1:200	Oct. 20, 1936	22.8	18.5 to 20.4	7.9	----------
		1:400	Oct. 21, 1936	22.8	20.1 to 20.7	7.9	----------
23	1.0035	1:1,000	Sept. 3, 1937	19.9	26.6 to 28.4	8.1	8.1
			Sept. 8, 1937	19.6	23.2 to 23.4	7.9	7.9
24	1.0043	1:500	Sept. 16, 1937	17.0	22.0 to 23.2	8.1	----------
		1:2,000	Sept. 24, 1937	21.7	20.3 to 21.3	8.1	----------
		1:4,000	Sept. 27, 1937	21.1	18.3 to 19.7	8.1	8.1
[1] 24	1.0043	1:500	Sept. 29, 1937	29.7	18.2 to 19.5	8.0	----------
			Oct. 6, 1937	----------	23.9 to 24.8	8.1	8.1
		1:1,000	Sept. 30, 1937	28.8	19.0 to 20.4	7.9	7.9
			Oct. 1, 1937	28.5	20.7 to 21.0	7.9	7.9
			Oct. 2, 1937	25.7	21.6 to 22.5	7.9	7.9
			Oct. 3, 1937	25.7	22.3 to 22.8	7.9	7.9
			Oct. 4, 1937	25.5	22.6 to 23.0	7.9	8.0
			Oct. 5, 1937	----------	22.8 to 24.9	7.9	7.9
		1:2,000	Oct. 7, 1937	----------	24.1 to 24.9	7.9	7.9
			Oct. 8, 1937	25.1	20.1 to 19.6	7.9	7.9
Paper-mill effluent							
52	1.0013	1:500	June 14, 1938	17.9	21.7 to 22.4	7.9	7.9
			June 15, 1938	18.6	22.6 to 23.5	8.0	8.0
57	----------	1:500	June 16, 1938	18.9	21.2 to 22.2	7.9	8.0
			June 17, 1938	19.5	23.8 to 24.8	8.0	7.9
62	----------	1:500	June 22, 1938	18.5	24.0 to 24.6	7.9	7.9
			June 23, 1938	18.7	24.8 to 24.4	8.0	----------
			June 24, 1938	18.3	25.3 to 26.4	7.9	7.9

[1] Tests at Beaufort, N. C.

experiments in which fixed concentrations of pulp- and paper-mill effluents were used are given in table 49. All samples of paper-mill effluent tested contained no physiologically active material.

Analysis of the experimental data shows that with the exception of high concentrations of 1:100 and 1:200 the depression caused by a given concentration of pollutant remains fairly constant for several hours and does not increase with the duration of the test (fig. 54). The inference can be made that, under the conditions of these tests, there was no cumulative effect of the pollutant on the ciliary mechanism of the oyster. Neither was there any indication that oysters become adapted to a given concentration and develop greater tolerance. This is of interest because it has been shown that, in chlorinated water, oysters easily develop tolerance to relatively high concentrations of free chlorine (Galtsoff 1946).

In order to obtain a better understanding of the relationship between the depressing effect of the pulp-mill effluent and its concentration and to avoid the difficulty caused by wide fluctuation in the specific gravity and toxicity of various samples, a series of tests was made using one sample (No. 24) which proved to be highly toxic. The sample was collected on September 19, 1937, and was stored in well-stoppered bottles. Its specific gravity was 1.0043 and the color of the liquid was dark brown. In conducting the tests, each oyster was exposed only once to a given concentration, in which it was kept for one and a half hours, and the velocity of the cloacal current measured at half-hour intervals. The rate of pumping before the pollutant was added was considered as representing the normal rate. Thus, the conditions of these tests were entirely different from those of the experiments summarized in figure 52. Namely, each oyster was left in the pollutant for one and a half hours instead of 15 minutes and was subjected to only one concentration instead of being exposed to the cumulative effect of gradually increasing concentrations.

The results, expressed in percentages of the normal rates of pumping, show a definite relationship between the concentration of the sample and its depressing effect (table 50). This relationship approximates a straight line (fig. 55). A comparison with

the results of other tests summarized in figure 52 shows that the depressing effect of sample 24 was more than ten times greater than that of the samples used in previous experiments.

TABLE 50.—*Depression of the rate of filtration caused by pulp-mill effluent (sample 24)*

[Specific gravity 1.0043. Carmine-cone method. Figures express means of percentages of normal rate. Each oyster was exposed to one concentration of the effluent for 1½ hours. Three sets of readings were made at half-hour intervals]

Concentration, parts per liter	Number of oysters	Percentage of normal rate	Standard deviation	Percentage of depression
0	21	100		0
.25	6	99.2	4.37±0.87	0.8
.5	18	89.2	8.21±1.90	10.8
1.0	27	77.8	5.83±1.12	22.2
2.0	15	36.5	5.65±1.46	63.5

It was thought that oysters in the lower part of York River, being exposed for a long time to very low concentrations of pollutant, may have developed a certain degree of tolerance and become less sensitive to pulp-mill effluents than oysters living in unpolluted water. To test this possibility sample 24 of the pulp-mill effluent was divided into two portions and a series of bioassays was made simultaneously at Yorktown, Va., and at the United States Fisheries laboratory at Beaufort, N. C. Details of

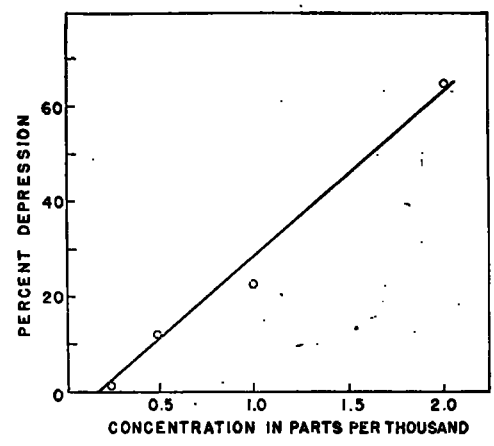

FIGURE 55.—Percentage of depression in ciliary motion of the gill epithelium, as measured by the carmine-cone method, caused by various concentrations of pulp-mill effluent (sample 24, specific gravity 1.0043).

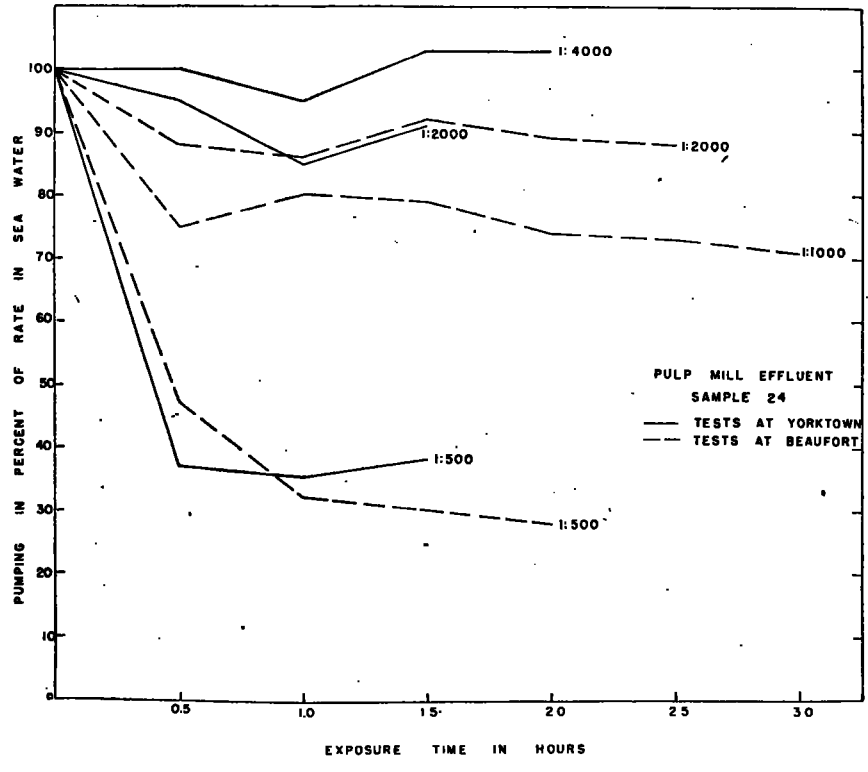

FIGURE 56.—Comparison of the effects of time of exposure of various concentrations of pulp-mill effluent on the rate of water filtration of oysters in tests carried on at Beaufort, N. C., and at Yorktown, Va. Tests were run at the same time at each locality and with the same sample of effluent. Two oysters and a control were observed for each concentration.

the two sets of experiments are given in table 49. As can be seen from figure 56, the behavior of the oysters from Beaufort, that had not been in contact with pulp-mill waste, was no different from the behavior of the oysters from the lower part of the York River, which for several years might have been subjected to very low concentrations of the pullutant.

From numerous observations with the carmine-cone method, we conclude that the presence of pulp-mill effluent exerts a definite depressing action on the ciliary epithelium of the gill and reduces its efficiency, the reduction in rate being proportional to the concentration of the physiologically active components of the pollutant. The effect is, however, temporary and the normal rate is restored soon after fresh sea water is supplied the oyster. There is no evidence that several hours of exposure to the concentrations used in the tests produce irreparable changes in the gill epithelium.

Experiments Using the Drop-Counting Method

This method (p. 133), differs from that of the carmine cone in two essential points. First, the oyster is kept in running sea water, which prevents the accumulation of the products of metabolism and, second, the rate of flow of the current produced by the gill epithelium is recorded automatically without disturbing the animal. It was therefore possible by using this method to obtain numerous records of the activity of the oyster in natural sea water and in various concentrations of test materials. As in the experiments previously discussed on the effects of river water of the upper York River on the ciliary activity of oysters, the kymograph records showing the number of drops of water discharged through the cloaca were analyzed for each 10-second interval of the period of recording, which usually lasted from 2 to 2½ minutes. The average figure thus obtained was multiplied by 60 to give the number of drops per minute. The temperature, pH, and salinity of the sea water were observed during the periods of testing and are recorded in table 51. Each experiment lasted from 4½ to 6 hours. In these experiments there was no recirculation of the test material as there was in the experiments described on page 133 in which the amount of test material available was small.

Material for testing comprised 11 different samples of pulp-mill effluent collected from sewers *J* and *H* and one sample of the material draining from the sludge pond. The results of the experiments are presented graphically in figures 57, 58, 59, and 60. They confirm the findings obtained with the carmine-cone method that the effluents arising from the pulping process depress the ciliary activity of the gill epithelium. The drop-counting records clearly show that, in physiologically active solutions, the effect is immediate. As the water containing pulp-mill effluent is turned on, the number of drops of water discharged through the gills decreases almost immediately. The normal rate is restored, however, as soon as the delivery of the pollutant is stopped. This can be easily noticed in figures 57 to 60 in which the beginning and end of each treatment are indicated by vertical black arrows.

Recovery after treatment is complete and, in many instances, the rate of pumping of water through the gills after the removal of the effluent is greater than it was before the treatment. We may conclude that the ciliated epithelium of the gills suffers no irreparable damage due to the presence of pulp-mill effluent, which apparently acts as a depressing or narcotizing agent. As soon as the latter is removed from the environment, normal function of the ciliated epithelium of the gills is fully restored.

Effect of Pulp- and Paper-Mill Effluents on the Rate of Pumping of Water by Intact Oysters (Rubber-Apron Method)

The object of employing this method was to observe the effect of pulp- and paper-mill effluents on the pumping activity of intact oysters exposed over long periods to various concentrations of the pollutants. While the carmine-cone and drop-counting methods are well adapted for the study of one isolated mechanism of feeding, the rubber-apron technique is suitable for determining the combined action of all the mechanisms which control the rate of water filtration by the oyster, namely, that of the ciliated epithelium of the gills and their ostia, the mantle, and the adductor muscle.

By using a constant-level tank (Galtsoff 1928) simultaneous records were obtained of the water output of experimental oysters subjected to pulp- and paper-mill effluents and of the control oysters in unpolluted sea water. Nelson's method (Nelson 1936) for preparing an oyster for such observation was used with modifications which permitted the gathering of continuous records of the rate of pumping and the shell movements. A piece of rubber dam was patterned to form a conical shape when wrapped around an oyster, the cone leading away

TABLE 51.—*Effect of pulp-mill effluent (sewers J and H) and sludge-pond effluent on the rate of discharge of water through the gills (drop-counting technique)*

[See figs. 58, 59, 60, and 61]

Sample No.	Specific gravity at 17.5° C.	Concentration	Effect on rate of pumping	Experiment No.	Date	Temperature °C.	Salinity ‰	pH
Pulp-mill effluent					*1936*			
3	1.0029	1:200	Depressed	8c	June 5	23.3	16.7	8.2
6	1.0012	1:400	do	13c	Nov. 12	15.6	22.3	8.0
19	1.0028	1:200	do	RF12 [1]	Aug. 12	21.4	31.2	
		1:500	do	RF 8 [1]	Aug. 18	21.2	36.9	
					1937			
24	1.0043	1:1,000	Depressed	15c	Sept. 19	24.2	18.6	8.0
			do	1	Nov. 1	15.0	14.6	8.1
			do	2	Nov. 2	16.1	16.9	8.1
			do	3	Nov. 3	15.2	16.8	8.1
			do	6	Nov. 5	15.4	17.4	8.1
		1:2,000	Depressed	7	Nov. 7	15.3	18.2	8.3
			do	9	Nov. 9	15.6	17.2	8.1
			do	12	Nov. 12	15.6	18.1	8.1
		1:500	do	17	Dec. 13	20.7	19.1	7.8
25	1.0025	1:1,000	Depressed	19	Dec. 14	20.5	18.8	7.8
			do	21	Dec. 15	20.7	18.6	7.9
			do	22	do	20.7	18.6	7.9
		1:2,000	Depressed	13	Dec. 9	20.3	15.1	7.9
			Not depressed	16	Dec. 10	20.1	17.6	7.9
					1938			
35	1.0038	1:500	Depressed	25	Feb. 15	21.4	19.4	8.1
			do	24	do	21.3	19.4	8.1
40	1.0040	1:500	Depressed	40	Mar. 8	22.5	20.5	8.0
			do	41	do	22.7	20.5	8.0
			do	42	Mar. 9	22.4	21.0	8.1
			do	43	do	22.4	21.0	8.1
			do	44	Mar. 10	22.2	20.4	8.0
			do	45	do	22.1	20.4	8.0
			do	46	Mar. 11	21.8	20.0	8.0
42	1.0020	1:500	Depressed	74	Apr. 20	20.8	17.1	7.9
			Not depressed	72	Apr. 11	20.1	16.6	7.9
			do	73	do	20.2	16.6	7.9
			do	75	Apr. 20	20.6	17.1	7.9
50	1.0022	1:500	Not depressed	90	June 6	22.5	18.1	8.0
			Depressed	91	June 7	24.1	17.4	8.1
			do	92	do	24.2	17.4	8.1
			do	93	June 8	22.9	17.4	8.1
			do	94	do	22.8	17.4	8.1
			do	95	do	22.8	17.4	8.1
			do	96	do	22.9	17.4	8.1
51	1.0014	1:500	Depressed	100	June 14	22.4	17.9	7.9
			do	101	do	22.2	17.9	7.9
			do	102	do	22.2	17.9	7.9
63	1.0013	1:500	Depressed	112	June 24	25.6	18.3	7.9
			Not depressed	113	do	25.6	18.3	7.9
Sludge—pond effluent					*1938*			
56	1.0026	1:500	Depressed slightly	105	June 15	23.0	18.6	8.1
			do	106	do	23.0	18.6	8.1
			Not depressed	107	June 17	23.5	19.5	8.0
			Depressed slightly	109	do	23.5	19.5	8.0
			Not depressed	110	June 21	23.5	17.4	7.9
			do	111	do	23.5	17.4	7.9

[1] Tests at Woods Hole.

from the out-current side. The rubber dam was cemented tightly to the oyster with sufficient slack at the posterior end to allow the valves to part freely and without obstruction. Into this slack region was inserted a plug of cotton to prevent any water escaping to the in-current side. The oyster, equipped in this manner, will, when feeding, discharge all water into the apron.

The oyster was then placed in a constant-level chamber and the end of the rubber cone firmly attached to an outlet trough about 1½ inches in diameter. The water pumped by the oyster was collected and measured by means of a dumping vessel which automatically discharged when the water reached the desired level. Each dumping was recorded on a slow-motion kymograph. Full description of this method with detailed diagrams is given in the paper of Galtsoff (1946), Reaction of Oysters to Chlorination.

By using this method, the rate of water filtration was measured in oysters kept in various dilutions of pulp-mill effluents for a period of time varying from 1 to 13 days. In each experiment two oysters were observed: one of them was kept in unpolluted water and served as a control, the other was placed in a known concentration of the pollutant which was

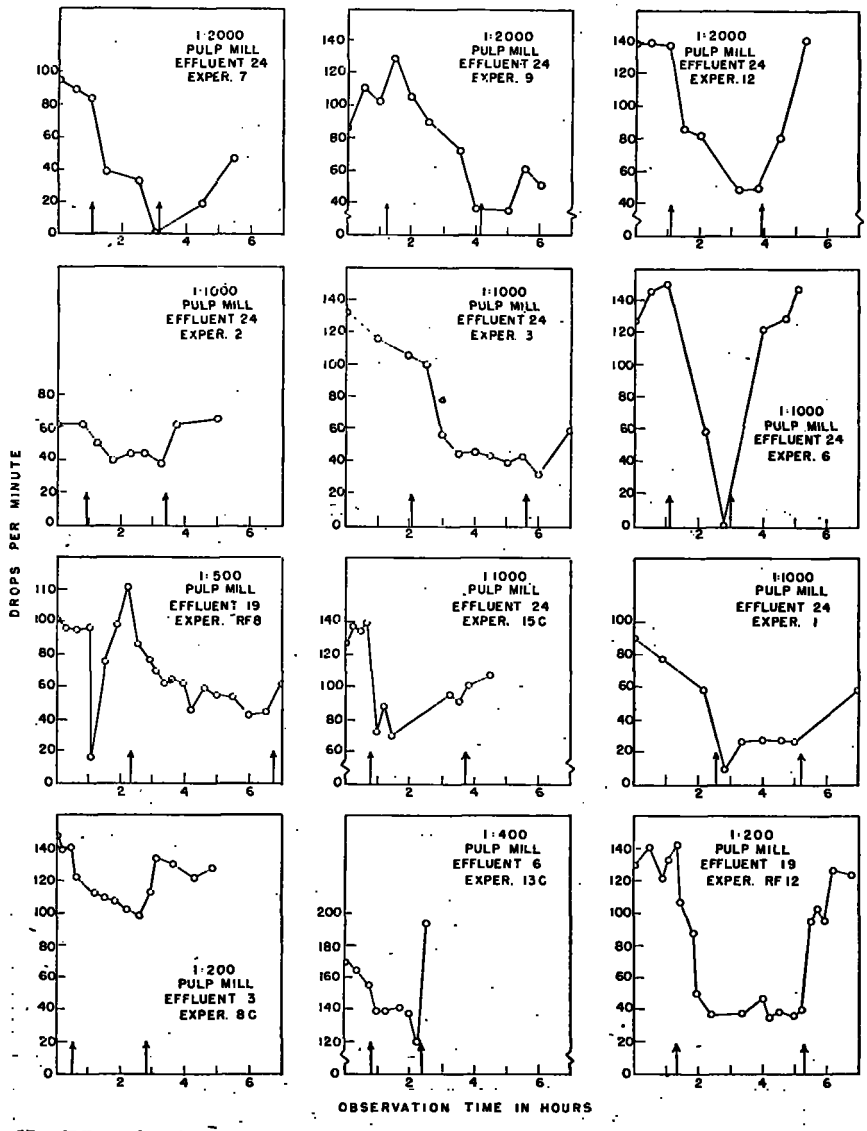

FIGURE 57.—Effect of various samples of pulp-mill effluent on the rate of filtration of water by oyster gills measured by the drop-counting method. Concentrations: 1:2,000; 1:1,000; 1:500; 1:400, and 1:200.

flowing through the chamber at the same rate as the unpolluted water that was delivered to the control. Records of the temperature and salinity of water were maintained. In every respect the control and test oysters received identical treatment except that the water supplied the control contained no pollutant. All of the oysters used were normal healthy specimens taken, in most cases, from the lower York River.

Before the beginning of each test, continuous record of the rate of pumping and of muscular movement of both oysters were obtained. In the majority of cases, this preliminary period lasted 2 or 3 days. Only in one instance was the test started 24 hours after the oyster was placed in the tank and in two instances the oysters were kept for 4 and 6 days before the pollutant was added. Numerous observations performed by Galtsoff at the Woods Hole laboratory in connection with a study of the physiology of feeding show that oysters wrapped in rubber-dam aprons and kept in constant-level tanks suffer no ill effects caused by their abnormal situation. If temperature and other conditions of water remain unchanged, the rate of pumping proceeds at a very constant rate. This can be seen also from the fact that by the end of the tests, some of which lasted as long as a fortnight (fig. 62), the rate of

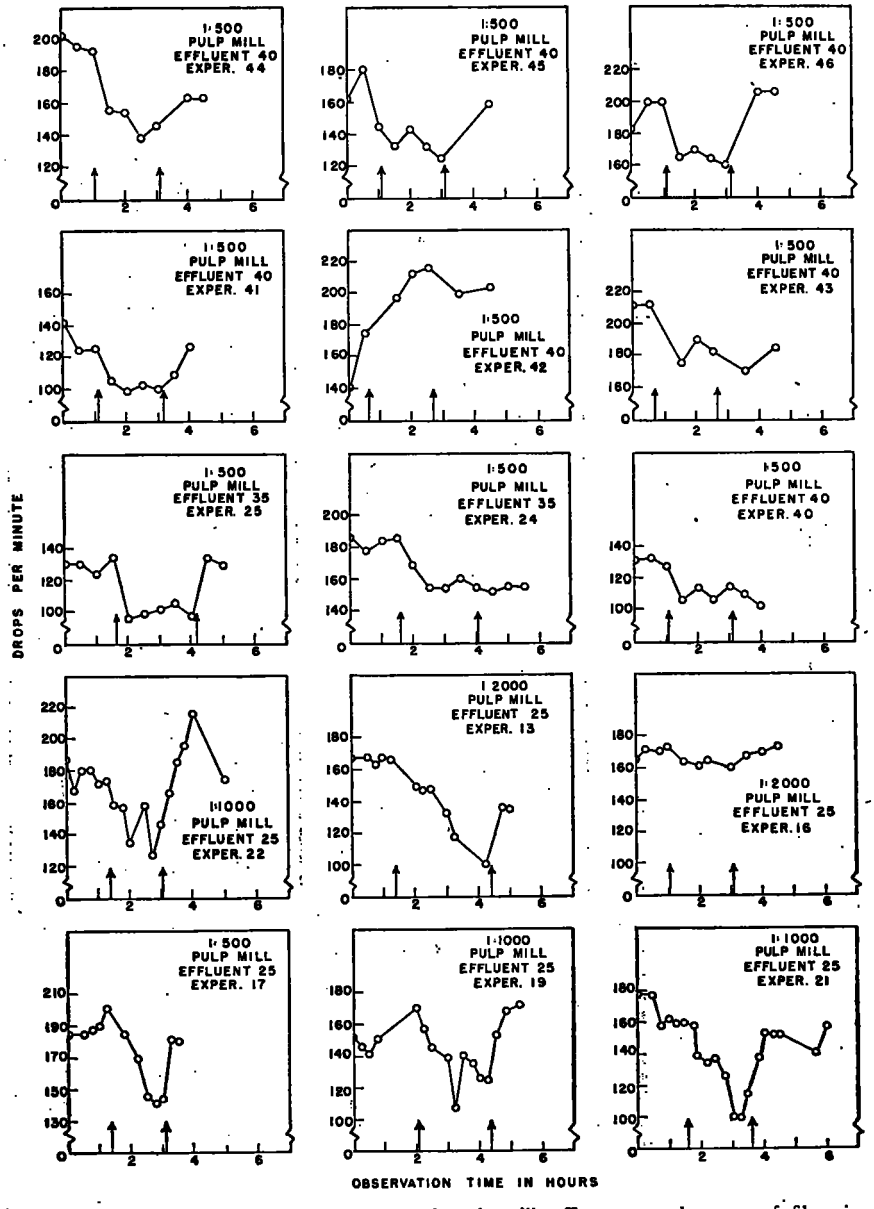

FIGURE 58.—Effect of various samples of pulp-mill effluent on the rate of filtration of water by oyster gills measured by the drop-counting method. Concentrations: 1:2,000; 1:1,000; and 1:500.

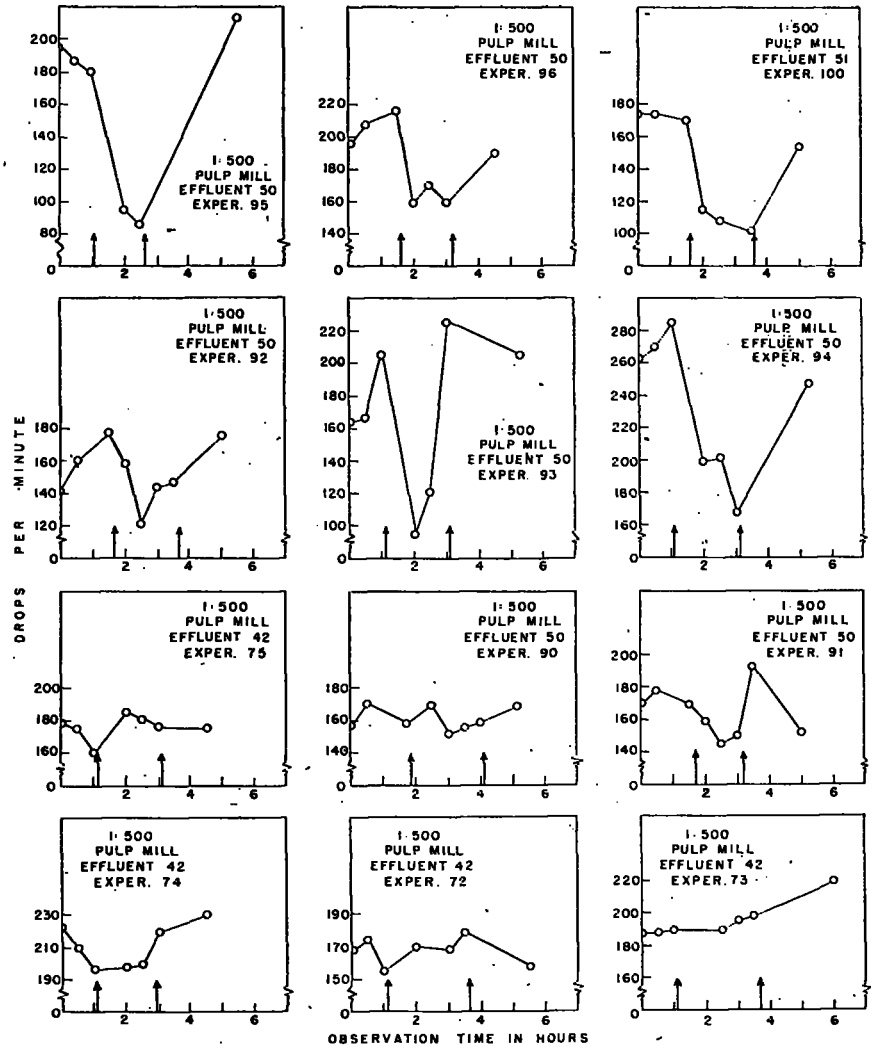

FIGURE 59.—Effect of various samples of pulp-mill effluent on the rate of filtration of water by oyster gills measured by the drop-counting method. Concentration 1:500.

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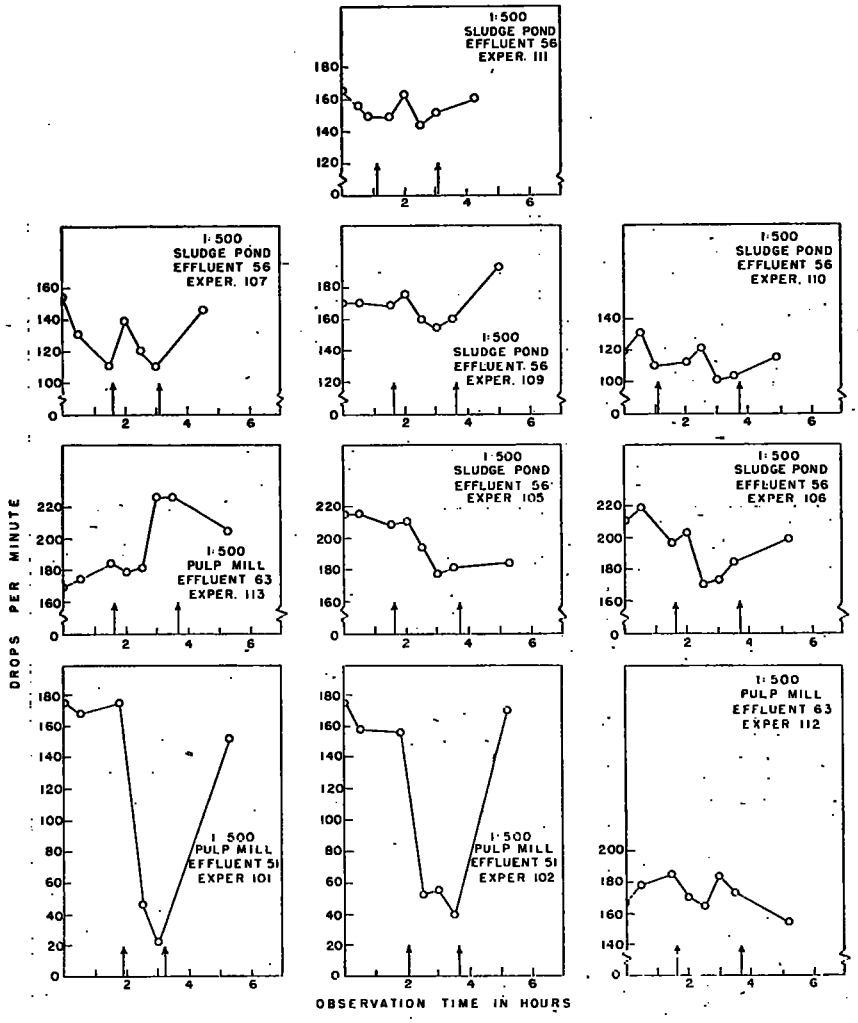

FIGURE 60.—Effect of various samples of pulp-mill and sludge-pond effluents on the rate of filtration of water by oyster gills measured by carmine-cone method.—Concentration 1:500.

pumping of water in the control oyster was approximately at the same level as at the beginning of the experiment.

Obviously, the larger oysters pump greater amounts of water than smaller ones, but besides the differences in size, the rate of pumping is dependent also on the physiological conditions or the needs of the organism. These conditions cannot be ascertained in advance. A study of the effect of an external factor on the rate of pumping must be made, therefore, by determining this decrease or increase in comparison with a certain known level of activity. This basic rate of pumping, which was considered as 100 percent, was determined for each experimental oyster by analyzing its record of activity during the preliminary period, i. e., when the test specimen was kept in plain sea water. Duration of these periods are given in column 8, table 52. From kymograph records the rate of pumping was determined for each hour the shells of the oyster were open and the mean rate for the entire period when the oyster was active was considered its basic rate. The mean rate of pumping in various concentrations of pollutant was computed in a similar way for the entire period of exposure, counting only the hours when the shells were open, and compared with the basic rate of the same specimen. Figures in the last column of table 52 give the percentages of the basic original rates. As can be seen from the examination of figures 61 and 62, the initial rates of pumping in the majority of oysters varied from 6 to 12 liters per hour. The purpose of the control

oysters was to demonstrate that no significant variation in the rate of flow could be attributed to some unexpected change in the sea water or to the injury of the oysters caused by the conditions of the experiment. Examination of the curves, marked in figures by solid circles, shows that the rate of pumping in the control remained fairly constant and, in many instances, was higher at the end of the test than at its beginning.

Concentrations of 1:200 and 1:400 of the pulp-mill effluent gave immediate and marked effects, depressing the water output to a small fraction of its rate observed before treatment. In the tests employing the concentration of 1:200 of samples 3 and 5, oysters filtering originally over 10 liters per hour, decreased the rate to a fraction of a liter (fig. 61). The effect of this effluent in concentrations of 1:770 and 1:1,000 was less pronounced. Some of the oysters were almost unaffected while others showed a marked drop in the rate of flow. Sample No. 6 decreased the pumping activity of one oyster at a concentration of 1:770 but did not appreciably alter the rate of another oyster kept in the same concentration. Of the six samples of the effluent tested at a concentration of 1:1,000, sample No. 6, which had the lowest specific gravity of the group, was the only one that did not produce a reduction in the rate of flow.

There was no change in the rate of pumping in the tests in which the paper-mill effluent (sewer *A*)

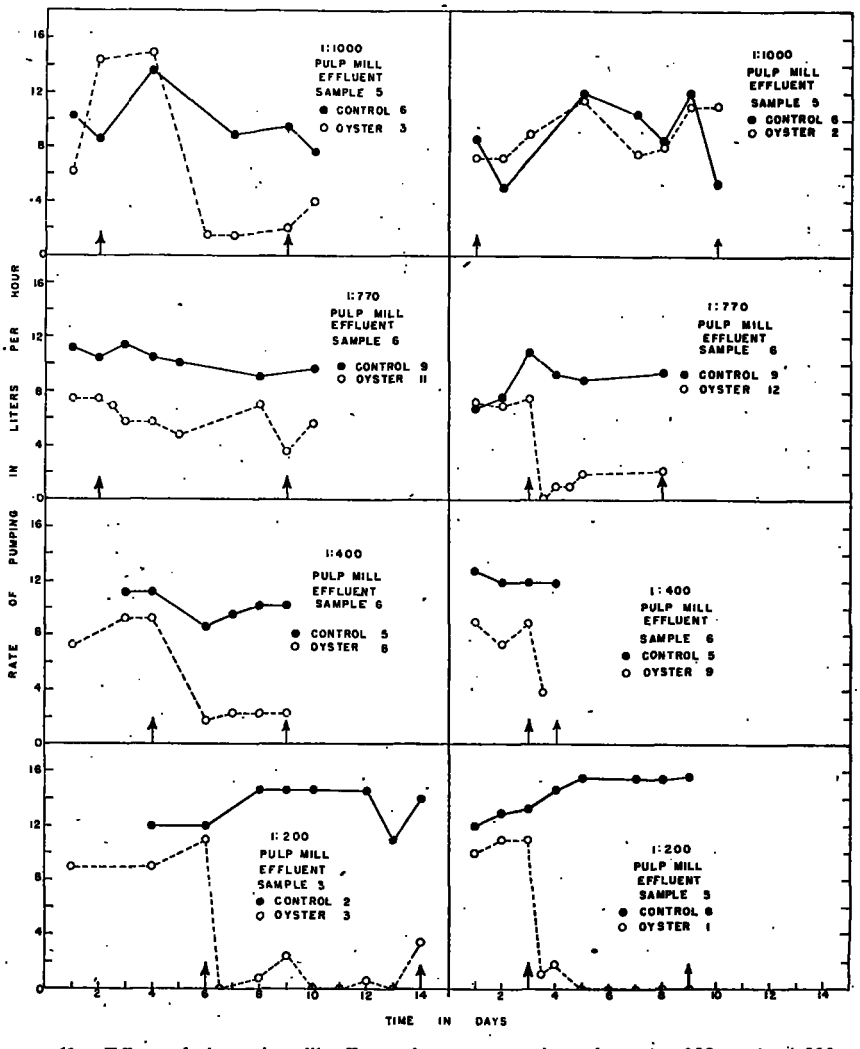

FIGURE 61.—Effect of the pulp-mill effluent in concentrations from 1 : 200 to 1 : 1,000 on the rate of water filtration of oysters. Rubber-apron method. The period between arrows represents the period of treatment. Conditions of the experiments are given in table 52.

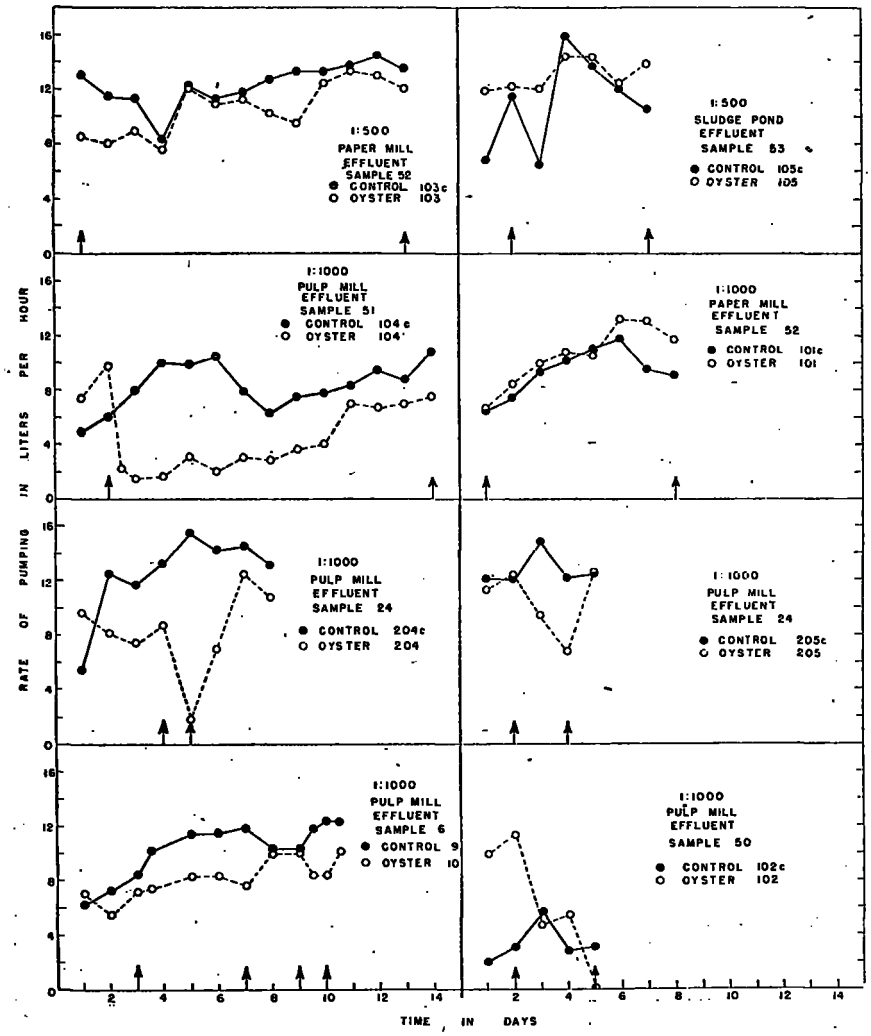

FIGURE 62.—Effect of pulp-mill effluent in concentrations of 1:1,000, paper-mill effluent in concentrations of 1:500 and 1:1,000, and sludge-pond effluent in concentrations of 1:500 on the rate of water filtration of oysters. Rubber-apron method. The period between arrows represents the period of treatment. Conditions of the experiments with pulp-mill effluent are given in table 52.

was used at concentrations of 1:1,000 or 1:500, nor with the sludge-pond effluent at a concentration of 1:500 (fig. 62).

It may be added that, in the tests with pulp-mill effluent, there was a noticeable change in the character of shell movement, consisting of a series of rapid and forceful closures (fig. 45) immediately after the addition of the pollutant. This reaction of the adductor muscle already has been described in a previous section. It was readily noticeable in the concentrations of 1:1,000 and stronger.

In several instances, when the pumping of water by experimental oysters stopped, the shells remained open, and the shell movement became irregular. These observations clearly show that the opening of the shell does not necessarily indicate that the oyster is feeding.

Experiments using the apron method clearly indicate that the physiologically active material was present in appreciable amounts only in the effluent coming from the pulping process (sewers *J* and *H*). They also corroborate the conclusion made from the tests using the carmine-cone and drop-counting methods that the amount of active material in different samples of pulp-mill effluent greatly varies.

So far, for the sake of convenience in presenting the experimental data, the various effects of pulp-mill effluent on oysters were considered separately.

TABLE 52.—*Effects of pulp-mill effluent (sewers* J *and* H) *on rate of pumping of oysters, (rubber-apron method)*

[Rate of pumping of test oysters is expressed in percentage of basic rate determined from records obtained during the number of days these oysters were kept in sea water before pollutant was added. Basic rate for control has been determined for the same periods of time. The order of figures of temperature and salinity indicates the trend of change during the test]

Concentration	Sample No.	Effluent specific gravity at 17.5° C.	Oyster No.	Dates of test (inclusive)	Temperature range °C.	Salinity range, parts per thousand	Days in sea water	Days in effluent	Rate of pumping in percent of original rate	
									Control	Test
				1936						
1:200	3	1.0013	1	Aug. 25–Sept. 2	29.0–24.2	21.9–23.2	3	6	119.1	4.4
1:200	3	1.0013	3	July 7–23	25.8–30.4	19.5–20.6	3	8	107.5	9.4
1:400	6	1.0012	9	Sept. 15–18	24.0–25.2	23.0–23.8	3	1	97.5	46.4
1:400	6	1.0012	8	Sept. 5–9	26.4–20.4	22.5–23.0	3	4	93.9	25.6
1:770	6	1.0012	12	Nov. 16–23	11.3–9.3	22.4–22.9	3	5	105.1	16.2
1:770	6	1.0012	11	Nov. 3–12	15.0–12.2		2	6	92.4	84.2
1:1,000	5	1.0013	3	Aug. 3–13	28.9–25.1	20.6–21.1	2	4	99.5	114.6
1:1,000	5	1.0013	2	Aug. 8–22	28.5–25.9	20.6–21.5	1	6	111.6	125.7
1:1,000	6	1.0012	10	Oct. 15–24	18.1–21.3	22.8–24.0	6	5	125.1	102.5
				1937						
1:1,000	24	1.0043	204	Oct. 22–29	17.5–13.0	20.7–19.9	4	1	128.2	22.1
1:1,000	24	1.0043	205	Nov. 7–11	14.9–12.3	17.2–18.4	2	2	110.4	70.7
				1938						
1:1,000	50	1.0022	102	June 8–12	22.6–25.3	17.1–18.8	2	3	156.0	39.9
1:1,000	51	1.0014	104	June 11–27	23.4–25.3	17.9–19.6	2	13	161.6	46.6

It has been demonstrated that the pollutant reduces the number of hours oysters remain open and depresses their rate of feeding. Either of these reactions reduces the amount of water filtered by the oyster. Their combined effect can be evaluated by determining from the kymograph records the total volume of water filtered by the oyster during each day of the exposure to the pollutant. As an illustration of such effect, we have selected the data from the test with oyster No. 104 which was kept for 12½ days in a concentration of pulp-mill effluent of 1:1,000. The specific gravity of the effluent was 1.0014 and the experiment was run from June 14 to June 27, 1938. During this time the temperature and salinity of water varied between 23.4° to 25° C. and 17.9 to 19 parts per thousand. The data are given in table 53.

During the first day and a half, when both the test and the control oysters were kept in plain sea water, the rate of pumping by the test oyster was slightly greater than that of the control. Both specimens were open for about the same number of hours. The rate of pumping and the total daily amount of water filtered was immediately reduced after the supply of the effluent was turned on. In the control oyster, the rate of pumping was gradually increasing and by the end of the test (fourteenth day of observation) this oyster pumped more than double the volume of water filtered during the first day. There was possibly some common factor present during the last 4 to 5 days of the test which was responsible for an increase in the rate of pumping of both oysters. The total result was that, during the 12½ days, the test oyster filtered 760.3 liters against the 2259.5 liters filtered by the control oyster, a difference of nearly 1,500 liters. Similar data computed for other tests show that the total amount of water filtered by the oyster is materially reduced when sea water in which they are kept contains small amounts of pulp-mill effluent.

TABLE 53.—*Effect of pulp-mill effluent (sample 51) diluted 1:1000 on the rate of pumping per hour and the total amount of water filtered by the oysters during each day in the experiments made June 14 to 27, 1938*

[Difference between control and experimental=1,499.2 liters]

Day of observation	Experimental			Control		
	Time open	Rate of pumping	Total water filtered	Time open	Rate of pumping	Total water filtered
	Hours	*Liters per hour*	*Liters*	*Hours*	*Liters per hour*	*Liters*
1	24.0	7.4	177.6	24.0	4.8	115.2
2 [1]	[1] 12.0	[1] 9.8	[1] 235.2	[1] 11.1	[1] 6.0	[1] 133.2
2 [2]	[2] 6.1	[2] 2.2	[2] 26.8	[2] 11.2	[2] 6.0	[2] 134.4
3	11.1	1.4	15.5	21.2	7.9	167.5
4	16.8	1.6	26.9	21.6	10.1	218.2
5	14.5	3.1	45.0	21.9	9.9	216.8
6	16.2	2.1	34.0	20.2	10.4	210.1
7	16.4	3.1	50.8	20.9	8.1	169.3
8	15.9	2.8	44.5	16.1	6.2	99.8
9	12.9	3.7	47.7	15.8	7.3	115.3
10	16.2	4.1	66.4	22.1	7.7	170.2
11	16.0	7.0	112.0	23.2	8.2	190.2
12	14.3	6.7	95.8	21.2	9.4	199.3
13	15.8	6.9	109.0	21.0	8.7	182.7
14	12.1	7.4	99.3	23.2	10.9	252.9
Total for 12½ days of test			760.3			2,259.5

[1] Observations made 12 hours before addition of test material to experimental chambers.

[2] Observations made 12 hours after adding of test material to experimental chambers.

PHYSIOLOGICAL EFFECTS OF VARIOUS MATERIALS CONTAINED IN THE PULP-MILL EFFLUENT

As all the pulp- and paper-mill effluents which exert a marked physiological effect on oysters were obtained from the outlet of the sewer connected with the pulping process, the physiological action of the various materials entering this sewer-ditch were made the object of investigation. The effluent of this ditch contains the following mill wastes: the last diffuser wash; sea water from the condensers; blow-down condensate; weak-black liquor; sulfate soaps; and "burnt cooks."

The first three are the normal components discharged through this sewer, while the last three enter at irregular intervals because of errors in the operation of either the digester house or of the recovery house. Before describing the manner in which these latter wastes find access to the sewers it is necessary to clarify the designations applied to some of these wastes.

The character of both the last diffuser wash and the weak-black liquor were given in connection with the description of the mill and its process, while the sea water is self explanatory.

The blow-down condensate arises as follows: after the cooking process has completely disintegrated the chips in the digester, the liberated cellulose fibers are released with the digester contents to the first cell of the diffusion battery. As the cooking liquor passes from the elevated temperature and pressure of the digester to the atmospheric pressure of the diffusion cell, it liberates great quantities of steam. This steam, which carries with it a large volume of vapors of volatile substances that are either liberated from or derived from the chips during the cooking process (Klason 1908; Klason and Segerfelt 1910; Bergström and Fagerlind 1909; Rinman 1911) is passed through a condenser in order to recover the turpentine present. After separation of the latter, the condensed water, or blow-down condensate, is discharged as a waste product into the weir.

The sulfate soaps may be described as follows: the species of wood used by this mill contain oleoresins (Herty and Dickson 1908) together with a certain quantity of the true fats (Carpenter 1937). During the pulping process the alkali of the liquor reacts with both the fats and the resin acids of the oleoresin, converting them into their respective sodium salts, which are ordinarily called soaps. These soaps, being but slightly soluble in the alkaline cooking liquor, tend to separate as an upper layer. That formed on the weak black liquor is known as "weak soap" while that separated in the process of concentrating the black liquor for incineration is called "strong soap." Despite their strong detergent power, these soaps are of little market value because of their dark color and disagreeable odor.

In most pulp mills there are occasions when, through some faulty procedure, the charge of chips in the digester undergoes, at the cooking temperature, a partial charring that results in a product called a "burnt cook," which makes the pulp obtained difficult to purify. Whenever the amount of charred material present is so great that the cost of purification exceeds the value of the usable pulp, the entire contents of the digester are usually discarded.

As black liquor, sulfate soap, and burnt cooks do not enter the sewer when the mill is operating properly, a description of their mode of entry is necessary, as all of them contain substances which exert a physiological effect upon oysters. Located in the area between the chip conveyor and the recovery house, but not shown in the plant lay-out in figure 4, are several covered steel tanks of different sizes which are used for the storage of black liquor during the various stages of its recovery. In the largest tank, about 30 feet in diameter, the filtered weak-black liquor is stored as feed for the evaporators. The air vent of this tank is connected to a 15-inch cast-iron pipe emptying into a weir in ditches *J* and *H*. The liquid in this tank is usually covered with a froth of weak soap which sometimes, if the tank is nearly full, can be seen escaping through the vent and flowing into the weir. On some occasions the weak-black liquor has been collected at the outlet of this pipe. Another, even more frequent, mode of entry of weak soap into the sewers *J* and *H* is the froth from the weak-black-liquor filter. This filter is on top of one of the smaller steel tanks located just outside the north end of building 9 in figure 4. This filter is fully enclosed, but fitted with a 4-inch vent pipe which discharges into an open sump beneath it. The position of this sump is about at the place in figure 4 where sewer *J* changes from a due north to a northwesterly direction. On almost every visit to the mill during the time of this investigation, this vent pipe was discharging a mixture of weak-soap froth and pulp fibers into the sump.

The strong sulfate soap gets into the sewers only

at very infrequent intervals, but the quantity entering at such a time is usually quite large. This strong soap, having been skimmed from the black liquor during concentration of the latter, is stored in one of the steel tanks previously mentioned. Steam coils in this tank keep the soap liquid so that it can be pumped to either the shipping dock or to the incinerators. The latter means of disposal requires high pressure in the pipe-line and occasionally there occurs a break in the line spilling the soap on the ground in the vicinity of these tanks. Between July 1 and November 1, 1938, no less than three such accidents occurred. Each time the spilled soap covered an area of more than a thousand square feet to an average depth of about 6 inches and extended to the sump. This soap, having very little value, is left on the ground until washed into the sump by rains, finally getting into the river. In the three cases observed it was apparent that at the time of the accident a large amount of soap had flowed into the sump.

Notwithstanding the claim that burnt cooks are not discarded, appreciable quantities of pulp are frequently found on the ground adjoining the weirs of sewers *J* and *H*. On one occasion, after the ditch carrying effluents from these sewers had been changed to a covered aqueduct, a pile of pulp 2 or 3 feet in diameter and 18 to 20 inches in height was found on the plank cover of the aqueduct where it connected with the weirs. The position of this pile of pulp in relation to the 15-inch cast-iron pipe which entered the weir, and the distance of the pile, more than 6 feet from the end of the pipe, indicated that the pulp had been discharged from the pipe with considerable force. These particles had a charred appearance typical of burnt cook, and were too black to be the shives usually found.

A few hours before this pile of pulp was examined, two 5-gallon samples of water, collected at the highway bridge over the Pamunkey River, about one-half mile down stream from the location of the outlet of the aqueduct carrying the effluent from this pipe, showed a marked physiological effect upon oysters and also contained considerable quantities of very black pulp.

For examination of the physiological effect, tests were made of strong soap, weak soap, weak-black liquor, last diffuser wash, and blow-down condensate, from samples collected as these materials actually were being added to the effluent of the pulp mill. For these tests the changes in the rate of pumping of sea water by oysters were observed using the carmine-cone technique as previously described, with increasing concentration of test material. The results are presented in figure 63.

From these results it will be seen that the materials effective in reducing the pumping activity of oysters are contained in the black liquor and soaps. These same materials, of course, are present in the last washings of the diffusers but here they are present in greater dilution and in only one of the experiments was this effluent sufficiently strong to produce a slowing down of the rate of pumping. It must be borne in mind, however, that the method of bioassay was such that the effective materials must produce their action within a 30-minute exposure time. No answer has been obtained, as to what action these physiologically active materials would exert on the oyster in dilute concentrations over a period of time. It will be readily seen, however, that these active materials do enter the river at times in very high concentration as a result of faulty operation of the equipment used in the recovery process. Some of the variations in the characteristics of both the pulp-mill effluents and mill liquors are given in table 54.

TABLE 54.—*Variations in mineral constituents of mill effluents and mill liquors*

Sample No.	Density $\frac{25° C.}{25° C.}$	Percentage by weight			Source of sample
		NaOH	Na_2CO_3	Na_2S	
70A	0.999	0.013	0.15	0.068	Outlet of 15-inch pipe (east weir of ditches *J* and *H*); weir full of froth.
71E	1.018	1.54	.54	.251	Weak-black liquor.
73	1.078	1.49	.64	.078	Do.
75	1.092	1.4	.67	.112	Do.
88	0.998	0.73	.12	.045	Outlet of 15-inch pipe (east weir of ditch *J* and *H*).
89L	1.056	0.57	.20	.13	Vent of 30-foot weak-black-liquor tank.
90	1.079	1.89	.60	.11	Weak-black liquor.
92	1.099	2.74	.98	.15	Do.
94	1.007	0.57	.23	.57	Outlet of 15-inch pipe (east weir of ditches *J* and *H*).
95	1.086	1.53	.44	.57	Weak-black liquor.
97	1.193	4.41	1.08	1.65	Concentrated black liquor.
98	1.083	1.86	.62	.74	Weak-black liquor.
99	1.015	2.20	.095	.071	Effluent of west weir of ditches *J* and *H*.

CHANGES IN EFFECTIVENESS OF PULP-MILL EFFLUENTS UNDER STORAGE AND OXIDATION

The usual effluents from the sulfate process freshly collected have been shown to contain substances having a marked physiological action on oysters and contain substances toxic to finned fishes (Hagman 1936). Since the materials are known to be oxidized (Bergström and Trobeck 1937) exposure of the pulp-mill effluents to the air for any appre-

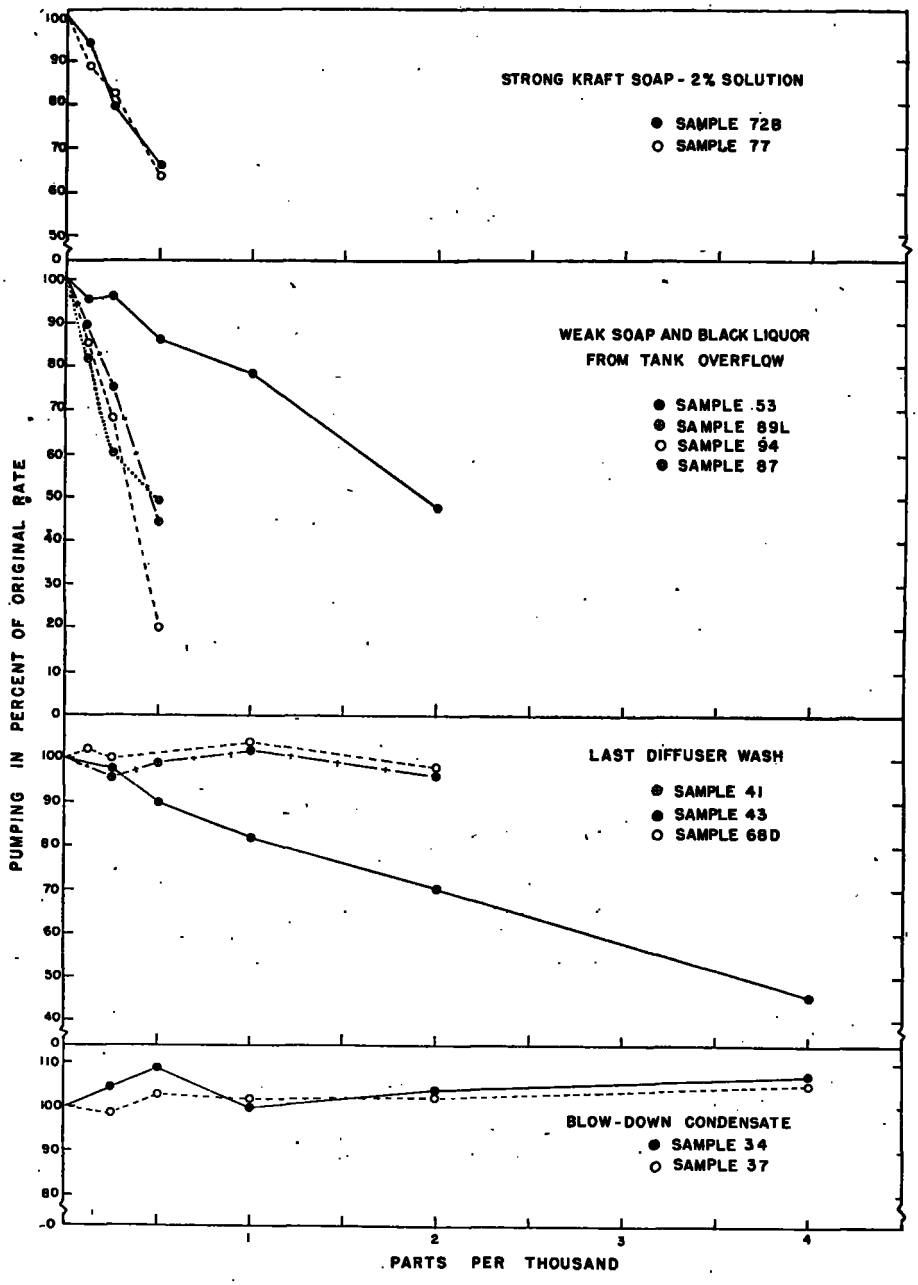

FIGURE 63.—Effect of various waste materials composing the pulp-mill effluent on the rate of water filtration of oysters. The exposure time was 30 minutes in each increasing concentration. Carmine-cone method.

ciable length of time might be expected to alter the character of the constituents present. As a consequence, experiments were performed to determine the changes in physiological effectiveness caused by the storage of the effluents and the effect of gases upon their toxicity.

A sample of effluent from pulp-mill sewers *J* and *H* was tested as to its effectiveness in reducing the rate of pumping of water by oysters. One portion of this sample was kept in a stoppered bottle and another in an unstoppered bottle open to the air for a period of 4 weeks. At the end of this period the stored portion was tested as to its action on oysters. The results, given in the curves of figure 64, show that storage under these conditions did not appreciably alter the physiological action of this sample.

Another sample of effluent from pulp-mill sewers *J* and *H* was collected and tested as to its action on oysters. One portion of this sample was dried at 35° C. in an open dish in an electric oven, and another portion was evaporated to dryness over a bunsen burner and then ashed. Both of the treated portions were then taken up in distilled water to their original volume and tested as to their physiological activity on oysters. The results are shown in the upper part of figure 64. Within the limits of these experiments, drying the sample greatly reduced its potency and ashing completely destroyed its activity.

Since the toxicity of the mill effluents was seen to be correlated rather definitely with the amount of weak-black liquor present, samples of weak-black liquor taken directly from the line supplying the evaporators were tested. The samples were collected into hydrogen-filled flasks. The flasks were completely filled with the hot liquor; then a rubber stopper connected to a hydrogen reservoir was inserted. After the stopper had been tied in place the connection to the hydrogen reservoir was opened. In this series of experiments, the stock samples were kept under hydrogen and for all withdrawals the liquid removed was displaced by hydrogen.

On the day of its collection a portion of this material was withdrawn in the manner described and tested as to its effectiveness in reducing the rate of pumping of oysters with increasing concentrations of the test material. At intervals, samples from the supply kept under hydrogen were withdrawn and tested. In the case of sample 90 (fig.

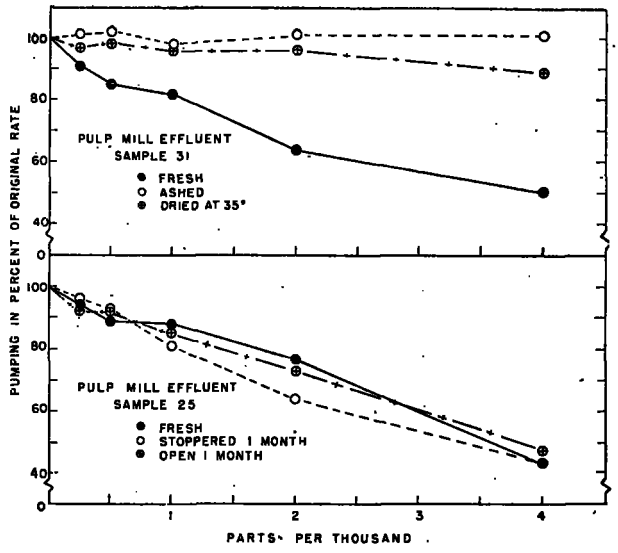

FIGURE 64.—Effect of storage and drying of pulp-mill effluent on its effectiveness in changing the rate of water filtration of oysters. Carmine-cone method with increasing concentrations at half-hour intervals.

65), storage under hydrogen completely prevented the loss in effectiveness of the sample for a period of 14 months. In sample 71E the loss in effectiveness was somewhat reduced, but the toxicity of the liquor was still pronounced after 14 weeks of storage (fig. 66).

In like manner, tests were made at intervals using portions of one of these samples stored in the laboratory in open vessels. The loss in potency with storage of the sample exposed to the air is seen in the different curves of figure 67.

On the day of its collection, a 250-milliliter portion of one of the samples was placed in a 500-milliliter flask; the superincumbent air was displaced with oxygen (99.5 percent purity) and the closed flask attached to a reservoir containing a known volume of oxygen. The flask and its contents were shaken for 90 hours. The absorption was at a pressure of 1 meter, water gage, and the oxygen consumption, not corrected to standard conditions, was 2,750 milliliters. Physiological tests with this portion showed that the potency had been completely destroyed by the treatment with oxygen. A graphic presentation of these data is given in figure 68.

From all the experiments performed, it is evident that by oxidation a great part of the active material of the effluent can be rendered physiologically ineffective. This material, however, is not readily oxidized. Storage in air for periods as long as eight

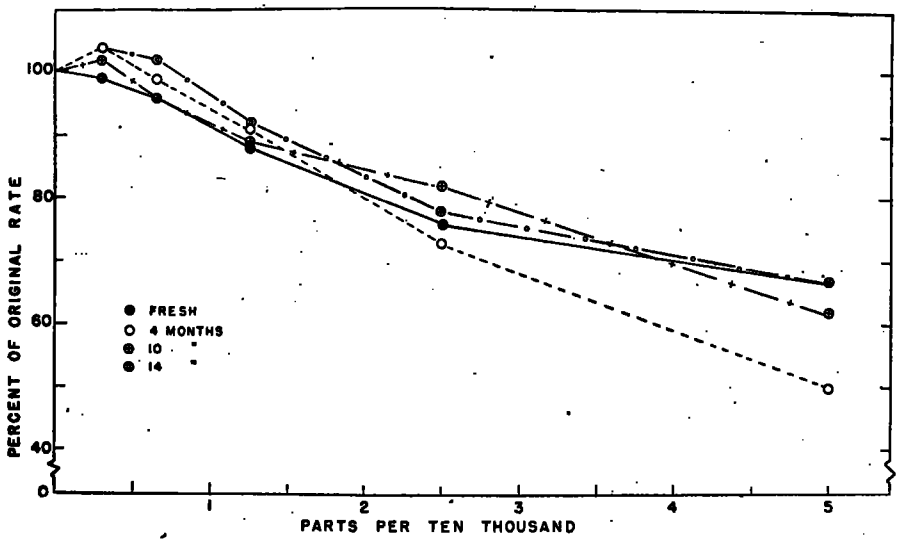

FIGURE 65.—Effect of storage under hydrogen on the effectiveness of weak-black liquor (sample 90) in reducing the rate of water filtration in oysters. Carmine-cone method; half-hour exposures to each of the increasing concentrations.

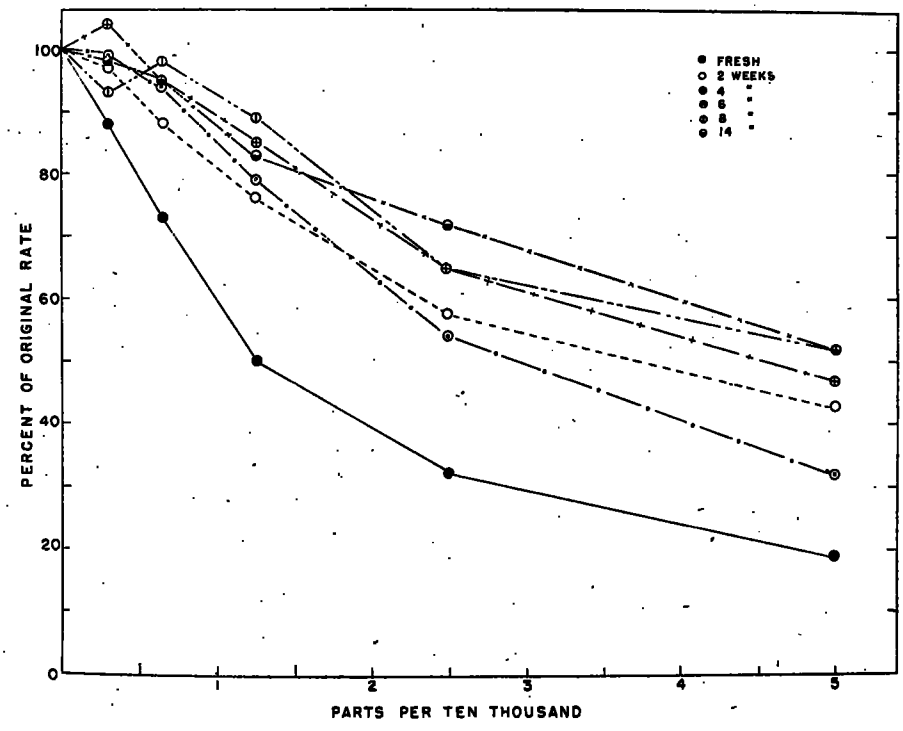

FIGURE 66.—Effect of storage under hydrogen on the effectiveness of weak-black liquor (sample 71E) in reducing the rate of water filtration in oysters. Carmine-cone method; half-hour exposures to each of the increasing concentrations.

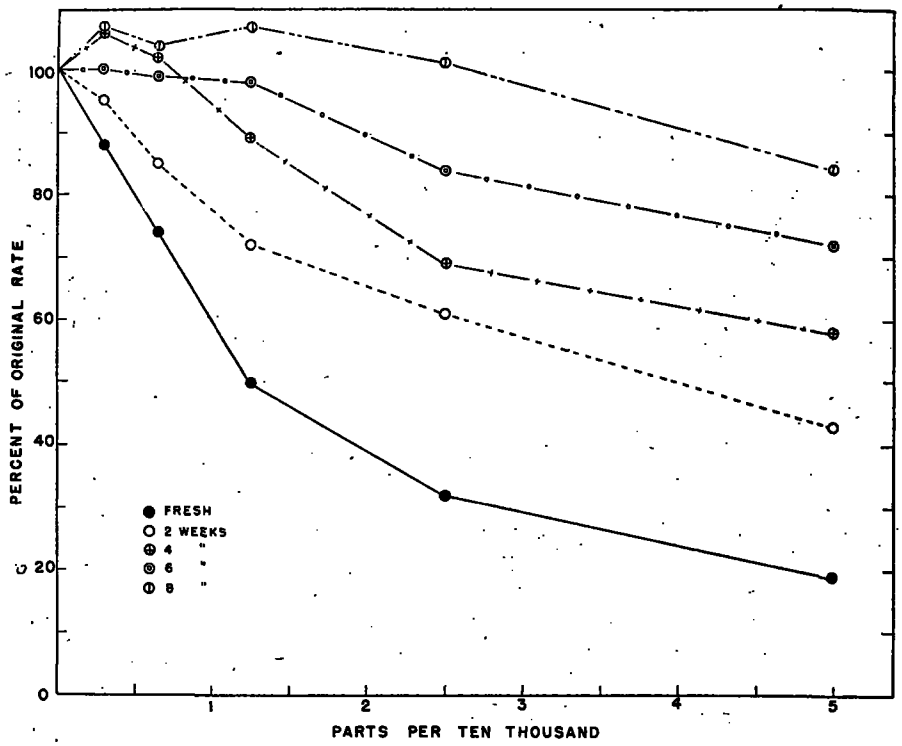

FIGURE 67.—Effect of storage in open vessels on the effectiveness of weak-black liquor (sample 71E) in reducing the rate of water filtration in oysters. Carmine-cone method; half-hour exposures to each of the increasing concentrations.

weeks did not completely destroy its effectiveness in reducing the rate of water filtration of oysters under the experimental conditions.

CHEMICAL NATURE OF WEAK BLACK LIQUOR AND KRAFT SOAPS AND RESPONSE OF OYSTERS TREATED WITH FRACTIONS OF THESE MATERIALS

Despite an extensive literature on sulfate black liquor very little of it deals with a careful determination of the organic constituents. Most of the publications are devoted to technical discussions of the processes advocated or in use for recovery of the alkali values from the liquor. The most frequently cited publications (Klason, 1893; Klason and Segerfelt, 1910) report lignin, ether solubles, formic, acetic, resin, and lactone acids together with phenols as the organic components. A similar paper (Klein, 1908) adds to the list but does not mention any sulfur compounds. In a discussion devoted chiefly to an improved pulping process, Rinman (1911) proposes a new classification of the gross organic constituents. In some fractionation experiments (Cirves, 1930) a relationship is sought between the pentose and hexose sugars and the oxyacids and humic acids of the black liquor. In a fairly recent paper (Heath, Bray, and Curran, 1933) attention is called to black liquor undergoing changes on storage.

A search (Holzer 1934) by the color-curve absorption method for the black-liquor constituents responsible for the dark color of sulfate pulp revealed a single, sulfur-containing, primary unit, which showed the reactions of phlobotannins, as being the source of the color. While the sulfur compounds in the stack gases from the incineration of the concentrated black liquor have given rise to numerous publications, there is only one (Kress and MacIntyre, 1935) in which attempts to prepare a sulfur balance for the sulfate-pulping process was made, but this paper gives no information about organic sulfur compounds in the black liquor.

The literature on sulfate soap is in a condition similar to that for black liquor, the principal topics being the development of refining processes which will enable the sulfate soap to be marketed in competition with soaps from the usual sources. The sulfate soaps from European sulfate mills have been studied by several workers, but, because of the difference in the tree species, the European data are

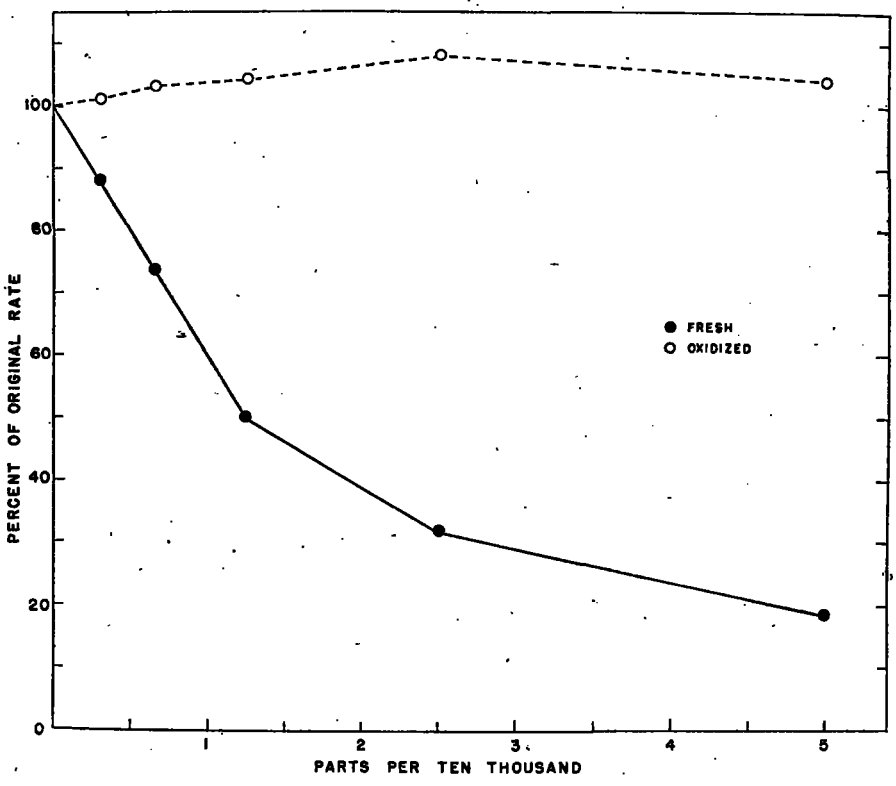

FIGURE 68.—Effect of treatment with pure oxygen on the effectiveness of weak-black liquor (sample 71E) in reducing the rate of water filtration in oysters. Carmine-cone method; half-hour exposure to each of the increasing concentrations.

of little value to the present problem. Three publications (McKee and Blengsli, 1936; Wallach, 1937; and Pollak, 1938) dealt with the composition of the sulfate soaps obtained in pulping American wood. The most comprehensive paper was that of McKee and Blengsli, who isolated from the soap acids a gasoline-insoluble substance which was not examined further than its classification as an organic acid produced by oxidation of the resin acids.

During the course of the present investigations fractionation was made of a sample of strong sulfate soap (sample 77) scooped from the ground in the area between the structures designated by the numbers 5, 9, and 10 in figure 4. During the night of October 30, 1939, the pipe line carrying the melted soap to the incinerators broke and spilled the soap on the ground. The total quantity of material spilled cannot be determined, but at 6 a. m. on October 31 the material covered an area of about 1,200 square feet and was still dropping to the ground from the broken pipe. At 11 a. m. the break had been repaired but the layer of soap had an average depth of about 8 inches over the area and remained there until rains carried it into the sump emptying into sewers *J* and *H*. At the time of the accident an unknown amount of this soap had also entered sewers *J* and *H* through the sump, for two sides of it were bordered by the spilled material. As shown in figure 63, a 2-percent solution of this soap produced a marked physiological action on oysters when added to the sea water in increasing concentration from 1 : 32,000 to 1 : 2,000. The sample was fractionated using methanol and ethanol in accordance with the scheme shown in figure 69, and the various fractions tested at like concentrations as the original sample 77 as to their effectiveness in reducing the rate of water filtration of oysters using the carmine-cone technique. The results of the bioassays of each fraction are indicated in figure 69. In control experiments it was learned that at the concentrations used with the sulfate soap fractions, both methanol and ethanol were found to have no physiological effect upon the oysters.

A study of the results shows that toxic substances are in that portion of the soap having the greater solubility in these solvents. The separation obtained

even with repeated fractionation was not capable of isolating the toxic substances in a highly concentrated form.

While treatment with strong alkali caused improvement in the color of the sulfate soap in agreement with the findings of Wahlberg (1924), it did not remove the toxic substances. Control experiments showed sodium hydroxide was physiologically ineffective except when present in high concentrations.

Although the strong sulfate soap contains material which has a physiological effect upon oysters, the concentrated black liquor after removal of the soap was found to be also effective.

As sulfate soap rarely flowed into the sewers its examination was discontinued in order to investigate materials that were discharged into sewers with greater frequency.

During the collection of the sample of soap just discussed a thick froth was being discharged from the vent and overflow of the weak black-liquor storage tank. Part of this material was dropping from the vent onto the ground and part was flowing from the outlet of the 15-inch cast-iron pipe in one of the weirs of sewers *J* and *H*. Two 10-quart pails were filled with material dropping from the vent (sample 89) and a 10-gallon tub was filled with the froth coming from the 15-inch pipe (sample 87). After standing, the greater part of the froth had liquefied. Sample 89 yielded about 1 liter (89L) and sample 87 about 6 liters. Each of these liquids when added to sea water in increasing concentration from 1:32,000 to 1:2,000 caused a physiological response in oysters as shown by a reduction in the rate of pumping.

Because of the small quantity available no attempts were made to fractionate sample 89L, but sample 87 was given an extensive examination which is recorded in figure 70. The various fractions obtained were tested at like increasing concentrations as to their effectiveness in reducing the rate of water filtration by oysters. The results of these observations are included in figure 70.

From each of these samples there remained a certain quantity of froth which had not liquefied even after standing for 48 hours. In the case of sample 87 this noncondensable foam when compacted

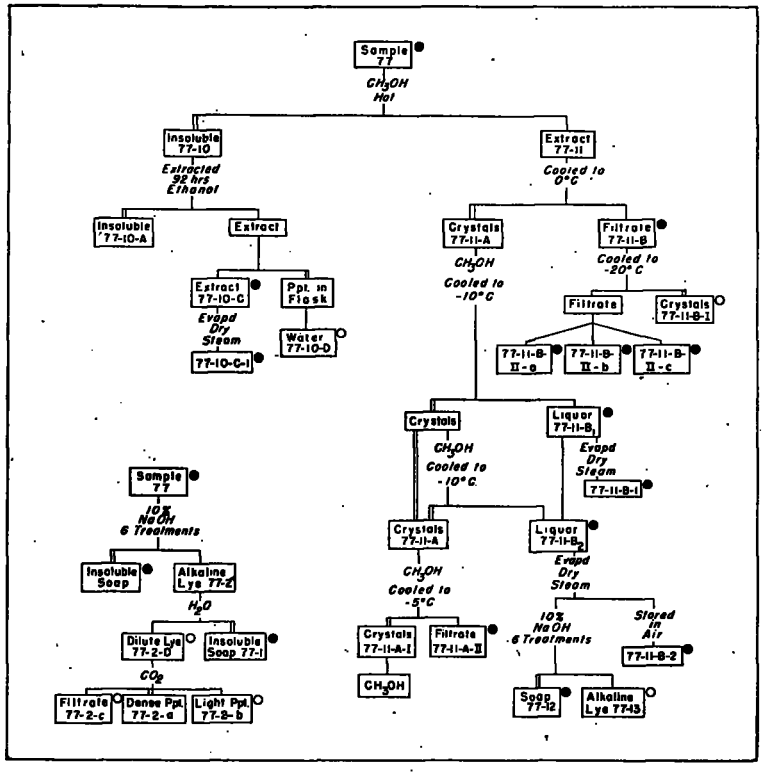

FIGURE 69.—Scheme of fractionation of strong Kraft soap (sample 77). The physiological effectiveness of the fractions is indicated by solid circles. Noneffective fractions are marked by open circles.

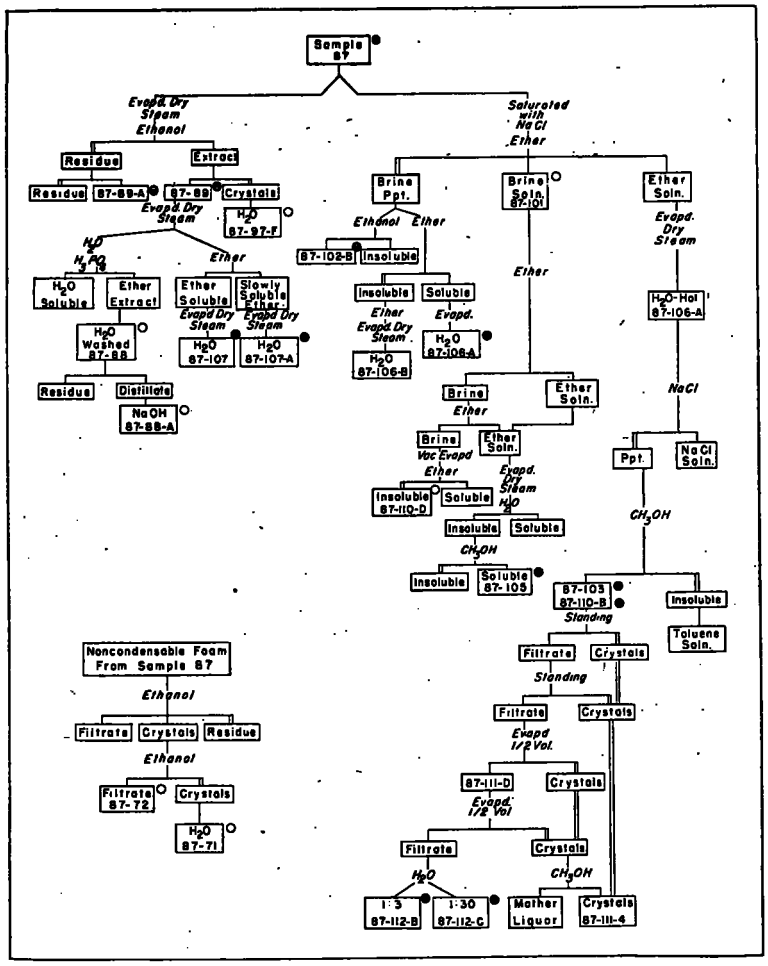

FIGURE 70.—Scheme of fractionation of weak soap (sample 87). The physiological effectiveness of the fractions is indicated by solid circles for effective, and empty circles for noneffective.

amounted to over 30 grams. This powder was extracted with ethanol in a Soxhlet apparatus. The sample was largely fine fibers and the extract did not yield fractions that were physiologically active. This fractionation, and its results when tested on oysters, is shown in the lower left section of figure 70.

Since concentration in vacuo of the liquefied portion of sample 87 was prevented by the excessive foaming due to the sodium soaps present, some of the liquid portion was evaporated to dryness in open vessels on a steam bath. The evaporation residue was then subjected to the fractionation shown in the upper left section of figure 70. It was shown in a preceding section that treatment of physiologically active mill effluents with gaseous oxygen destroyed the active principle and there was considerable likelihood that exposure of the original liquid material of sample 87 to air during evaporation might also bring about some oxidation of the active principle. This exposure to air during evaporation occurred with only the original material. All extractions of the evaporation residue and all subsequent evaporations as shown in the diagrammatic outline were carried out under hydrogen.

A portion of the liquefied material from sample 87 was saturated with salt in order to precipitate the soaps present and thereby enable evaporation to be carried out under reduced pressure and with the exclusion of air. The salt treatment precipitated the soaps as a finely divided suspension, but the addition of sulfuric ether caused them to concentrate in the upper layer. The products obtained as a result of the combined salt and ether treatments

of the liquefied portion of sample 87 were then fractionated in accordance with the scheme shown diagrammatically in the right-hand section of figure 70. As the results obtained supplied an important clue to the nature of the physiologically active materials present in the mill liquors, a detailed discussion of this fractionation will be given. Whenever possible the manipulations were performed in an atmosphere of hydrogen.

The combined treatments with salt and ether yielded three fractions. The precipitate consisted largely of soaps but it also contained other substances and some fine fibers. The ether layer was dark brown and contained the physiologically active materials, while the aqueous layer, besides being saturated with salt, contained materials which imparted a deep-red color to the liquid. The aqueous layer, after removal of the precipitate and the ether solution, was given two additional extractions with ether and was then concentrated without difficulty, under reduced pressure, to about one-third of its original volume. This concentration precipitated a large quantity of the salt, which was removed by filtration and washed twice with ether. These ether washings were now used to extract the residual liquor from the concentration of the aqueous layer and then combined with the other ether extractions of that layer. This residual aqueous solution and the original aqueous layer were bioassayed as fractions 87–110D and 87–101, respectively. The various ether extracts of the aqueous layer (87-101) and its fractions were combined and evaporated to dryness leaving a slight amount of a dark brown residue. When the residue from the evaporation of the ether extracts was treated with water, a small quantity of an insoluble oil arose to the surface. Filtration through a moistened filter separated the oil from the aqueous solution. Salt was the only material that could be isolated from the latter. The oil was treated with methanol giving an insoluble portion too small for further work and the fraction 87–105 of figure 70.

The salt precipitate, labeled "brine precipitate" in figure 70, was filtered from the ether required for coagulation and then given two additional extractions with ether. These two latter extractions, 87–106A and 87–106B in figure 70, were later combined with the ether solution from the coagulation treatment and the entire mixture was bioassayed as fraction 87–106A. The ether insoluble portion of the salt precipitate was now extracted with ethanol in a Soxhlet apparatus. After this treatment, there remained a small quantity of insoluble material consisting of fine wood-fibers. The ethanol extract was bioassayed as fraction 87–102B of figure 70.

When treated with water the ether residues 87–106A and 87–106B formed a light-gray emulsion. After some preliminary titrations a 10 percent salt solution was added in the proportions 6:10 breaking the emulsion and forming a gray precipitate which was separated and then leached with boiling methanol, leaving a grayish-brown residue soluble only in boiling toluene. Due to the insolubility in water of both the fraction and the solvent no bioassays were made. The methanol leachings were clear at first but on standing deposited a few crystals. As filtration and further standing yielded a few more crystals, the methanol solution was evaporated to about one-half its original volume and cooled, whereupon another small crop of crystals appeared. Filtration and further concentration of the filtrate gave a fourth deposit of crystals. These last were yellow whereas the earlier deposits had been white, but a recrystallization from methanol yielded a product similar to the others. These four deposits had a total weight of 0.09 grams, an amount too small for bioassay.

When the mother liquor from these crystals was diluted to four volumes with water, 87–112B, it caused a pronounced physiological action on oysters. Even after a further ten-fold dilution this material, 87–112C, still greatly reduced the rate of water filtration of oysters. The quantities of these samples remaining after the biological and chemical tests had been made were insufficient for further refining and testing, and the quantity of sample 87 on hand was too small to permit a repetition of the fractionation.

The method of salt precipitation used so successfully for separating the toxic portion of sample 87 met with several obstacles when applied to samples of weak black liquor. Due to the black liquor containing larger percentages of the constituents insoluble in the salt brine, the use of even larger volumes of ether did not effect a distinct separation between the brine and the precipitate. Filtration of such a mixture, using air-tight vessels filled with hydrogen, required several days and resulted in the loss of much of the ether from evaporation. Drying the material by storage over calcium chloride in hydrogen-filled desiccators required several weeks and caused the material to lose its physiological activity. When

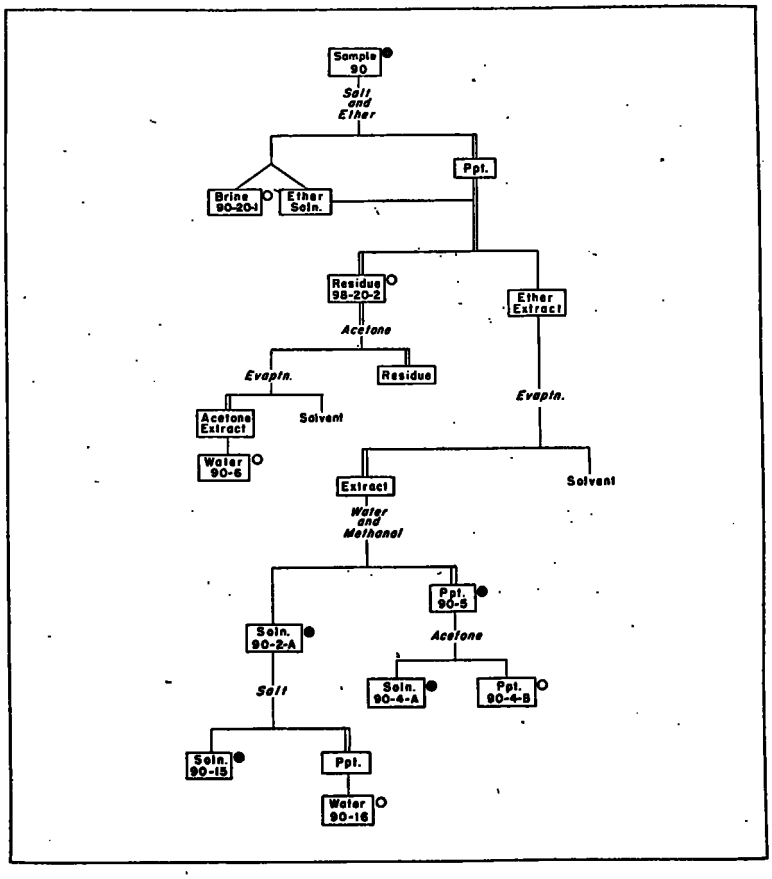

FIGURE 71.—Scheme of fractionation of weak-black liquor (sample 90). The physiological effectiveness of the fractions is indicated by solid circles for effective and open circles for noneffective.

placed in an evaculated desiccator the freshly precipitated material at once overflowed its container and filled the entire desiccator with froth. Partial drying over calcium chloride in a hydrogen-filled desiccator followed by the application of suction caused a sudden efflorescence of the precipitate and its loss by dispersion throughout the vessel. Despite continuous and vigorous shaking for 48 hours with much more salt than was needed to completely saturate the black liquor, a single treatment did not fully precipitate the toxic substances. After filtration, two further shakings with salt, each followed by filtration, were required to obtain a nontoxic filtrate from weak black liquor. These precipitates always retained a considerable quantity of the original black liquor taken for treatment because of their gelatinous character.

In view of the difficulties described, the following procedure was used in preparing precipitate for extraction. The weak liquor was shaken for 24 hours with salt and ether, then, filtered as rapidly as possible under hydrogen. This process was repeated for a total of three treatments. It was necessary to have ether present during the precipitation because the precipitates formed in its absence were so hydrophilic that the solvent could not "wet" them enough to effect solution of the toxic substances. The toxic materials in these precipitates were isolated by continuous ether extraction for seven days in a hydrogen-filled Soxhlet apparatus. The details of the fractionation and the results of the bioassays of the various fractions isolated from weak sulfate black liquor are given in figure 71. Increasing concentrations from 1 : 32,000 to 1 : 2,000 were employed in the physiological tests on oysters.

No extensive discussion will be given of the various fractions since it would parallel very closely that already given for sample 87. Only the fraction 98–20–2 needs comment. To conserve time this fraction was prepared from black liquor sample

98 and tested while the corresponding fraction of sample 90 was undergoing the further fractionation shown. While the results obtained with the weak black liquor are not as clear cut as those obtained with sample 87, they do lead to the same general conclusion.

CHEMICAL NATURE OF THE PHYSIOLOGICALLY ACTIVE MATERIALS IN SULFATE PULP-MILL EFFLUENTS

A study of the specific sulfate pulp-mill products which exert a physiological effect upon oysters leads to the conclusion that the toxic material tends to concentrate in the soap portion of the mill products. European investigators (Ebeling 1930, 1931, 1932; Bergström and Cederquist 1937; Bergström and Trobeck 1937; Bergström and Vallin 1937; Hagman 1936, 1937; Järnefelt 1936; Vallin 1935; Vestergren 1938) have arrived at similar conclusions concerning the toxicity of sulfate pulp-mill wastes to finned fishes, ascribing the toxic action to the resin acids and their sodium and calcium salts.

It has been found, however, in the work reported here that the sulfate soaps precipitated from mill liquors by salt were not toxic after treatment with ether, whereas the ether extracts of these soaps did contain the harmful material. This indicated that these soaps, when precipitated from aqueous solution by salt, adsorbed the toxic substance of the mill liquors. The necessity of repeated treatment of the black liquor with salt, before complete removal of the toxic substance was effected, is a further indication that its presence in the soap is due to adsorption by the latter of material "salted out" of the black liquor by the treatment with salt.

The sodium compounds in the black liquor will produce an effect similar to the action of the salt. Sample 87 also gave corresponding results, although to a lesser degree, in that the ether extract (87–105) from the concentrated salt brine also contained toxic material.

The exact nature of the toxic material has not been determined, but the readiness with which ether removes it from the soap leads to the opinion that we are dealing with a constituent of the unsaponifiable portion. It has been shown definitely by Erdtman (1939) that the toxic substance in the case of the European pine, *Pinus sylvestris*, is a dioxystilbene present in the heartwood of the tree. No such work has ever been undertaken upon the loblolly pine, *Pinus taeda*, although the durability of its heartwood has been recorded by Mohr (1897).

DISCUSSION AND CONCLUSIONS

Studies of the cycles of temperature, salinity, currents, oxygen content, pH, and plankton, described in the first part of this report, show that from an ecological point of view, the conditions in the York River follow the seasonal changes commonly encountered in tidal waters of the Atlantic coast. No abnormal deviation in these factors has been noticed during the course of the studies. It is true that the oxygen content was somewhat diminished in the upper part of the York River but the decrease was insignificant and cannot be considered as affecting oysters which are known to tolerate low oxygen tension (Galtsoff and Whipple 1931). The potential food supply for oysters, measured by the total production of plankton, was greater in the York River than in the Piankatank River. Thus, an assumption that the lack of food for oysters was responsible for their failure to fatten in the York River cannot be corroborated by the evidence and, therefore, must be discarded.

Observations on glycogen cycles in the York River oyster and field experiments in transplanting oysters from the upper part of the river to its lower part and (pp. 118–123) indicate the existence in the upper part of York River of an environment decidedly harmful to oysters. This harmful effect is manifested in the failure of oysters to accumulate glycogen, in a generally emaciated condition of their meat, and in the disturbance of the calcium metabolism which results in the abnormal condition of the shell.

Further proof that the upper part of York River provides an unhealthy environment is given by the results of the field tests in which the James River seed oysters, planted simultaneously in the upper and lower York River and in the Piankatank River (fig. 36), fattened much more rapidly in the last two localities.

Recovery of oysters taken from the upper part of the York River and transplanted to other waters indicates the presence of some toxic factor in the upper York River which does not occur in adjacent localities. If the poor condition of the oysters in the upper part of York River was due to infection by *Nematopsis* spores, disease, or to degeneration of the stock, one would not expect their rapid recovery after they were removed from the grounds and planted in the lower part of the York River or in the Piankatank River. The question naturally arises

whether the presence of foreign substances introduced in large quantities with the pulp-mill effluents at the head of the river at West Point is responsible for the pathological condition of the oysters. Direct evidence of the harmful effect of the pulp-mill effluent is provided by the physiological experiments which prove its toxicity. The deleterious action of the effluent is manifested by its effect on the adductor muscle, on the ciliary epithelium of the gills, and on the complex pumping mechanism of the oyster. By decreasing the number of hours the oyster stays open, the presence of the effluent in the water reduces the time normally used by the organism for feeding. Furthermore, the rate of feeding is also decreased because of the depression of the ciliary movement and reduction in the pumping capacity of the organism, due to the presence of the pulp-mill effluent.

The toxic agent in the effluent of the pulp mill produces a general depressing effect which inhibits the principal functions of the organism and results in its failure to accumulate glycogen and probably is responsible for the stunted growth of the oysters in the polluted area. This effect is apparently noncumulative, since under the conditions of the experiments, the oysters showed remarkable recovery immediately after their removal to unpolluted water. Their glycogen content increased to the normal level, shells were strengthened by deposition of lime, and growth was resumed.

The second question is whether the pulp-mill effluent occurs in York River in concentrations which were found to be effective in laboratory experiments. No chemical test is available at present for the detection and quantitative determination of the pulp-mill waste in natural waters. A nitrosolignin reaction developed by Pearl and Benson (1940) for sulphite waste liquor was not known at the the time the investigations were carried on in York River. Even if this method were known, its application in determining the concentration of pulp-mill effluent in York River would be of doubtful help because of the possibility that some of the nitrophenols which produce specific color reaction may be normally present in river water. Direct proof that harmful substances are present in the water of the York River was obtained by collecting samples of water in the upper part of York River at the time when a considerable area of the river was discolored by waste products discharged from the sewers of the pulp-mill plant at West Point, and using these for bioassays (p. 132).

Judging by the condition of the oysters in the lower part of York River and their ability to accumulate substantial amounts of glycogen, the deleterious effect of pulp-mill effluent extends down the river as far as Allmond's Wharf. It is, of course, of great interest to determine what concentration of pulp-mill effluent may actually occur in the upper half of the river and whether this concentration is of the same degree of magnitude as that which proved effective in the laboratory experiments. The problem presented considerable difficulties because of the great fluctuations in the rate of the discharge of the pulp-mill effluent and the changes in its specific gravity, presumably as a result of the degree of its dilution, chemical composition, and age. Using a conservative figure for the rate of discharge, based on personal observations, and knowing the resulting rate of flow of the river, it was possible to compute this concentration. Calculations made by using Hotteling's formula or employing the formula proposed by Tuckerman (p. 101) gave comparable results showing that either formula may be applied in such a problem.

In order to arrive at the mathematical solution of the problem, it was necessary to assume that the pulp-mill effluent is being discharged at a uniform rate, that it is rapidly and thoroughly mixed with the water, and is uniformly distributed in the river. It is realized that these assumptions deal with a more or less theoretical case and that, under natural conditions, the pulp-mill effluent is not discharged at a uniform rate and is not thoroughly mixed in the river but probably follows a definite path along the river axis. The above-mentioned assumptions have to be made, however, in order to solve the mathematical problem. It appears significant that theoretical calculations of the final concentration of the pulp-mill effluent in the polluted part of York River give a figure of 0.0004 or 1 : 2,500, which is of the same degree of magnitude as the threshold concentration determined by various laboratory tests. Thus, it has been shown that with the existing flow of the river and the observed rate of discharge of pulp-mill effluent effective concentration of the effluent may be expected to occur in the York River. Furthermore, the computations show that with a given rate of discharge of pulp-mill effluent at about 4.26 acre feet per day, this final concentration is reached within 100 days.

Laboratory tests, consisting in a study of shell movements of oysters, the efficiency of the ciliated epithelium of the gills, and the rate of pumping of water by the intact oysters, have demonstrated that pulp-mill effluent exerts a general depressing effect on the physiology of the oyster. It reduces the number of hours the oyster remains open and therefore decreases the time which could be used for feeding. It also reduces the rate of pumping of water by the gills. The depression of the rate of filtration is proportional to the concentration of the effluent. In case of the shell movement of the oysters and their ability to keep their valves open, the relationship between the concentration of the effluent and the mean number of hours the oysters remain closed can be expressed by an exponential equation (p. 141). The threshold concentration of the effluent, as determined by laboratory tests, is about 1 : 2,000. Because of considerable variation in the specific gravity and chemical composition of the effluent, this concentration does not remain constant and therefore could not be determined with accuracy.

Chemical studies of the pulp-mill effluent show that a physiologically effective fraction of black liquor which is found in the pulp-mill effluent can be separated by the method of salt precipitation. It was found that separation between the brine and the precipitate was rather difficult and that the toxic material had a tendency to concentrate in the soap portion of the mill products.

Sulfate soaps precipitated from mill liquor by salt, contained toxic material which apparently was adsorbed by them from the black liquor. Treatment with ether rendered these soaps harmless, whereas the ether extract was toxic. We may infer from these results that when black liquor is present in sea water a portion of it may precipitate as a soap and carry with it a certain portion of the toxic component. It is, therefore, quite possible that a certain portion of toxic material is carried down the river as precipitate and is deposited in the areas of sedimentation. This possibility provides a clue for explaining the rather puzzling fact that the poorest oysters were found not in an extreme upper section of the York River, close to the source of pollution, but several miles downstream on the grounds of Purtan Bay. Studies of the sedimentation process in the York River made by the Soil Conservation Service at the request of the Chesapeake Corp. (Brown, Seavy, and Rittenhouse, 1939) throw light on the problem. This investigation shows convincingly that:

> Between 1857 and 1911, there were two main areas of heaviest sediment accumulation, one at the head of the estuary between ranges 6 and 8, and one in the upper middle estuary between ranges 10 and 14. These areas of excessive accumulation were separated by an area of scour near range 9. A second and larger area of scour was located below range 14. Between 1911 and 1938 there were still two areas of filling and two of scour. These areas, however, coincide only partially with the areas of scour and fill between 1857 and 1911. The point of most rapid accumulation migrated downstream from range 13 to range 14, and sedimentation was also rapid at ranges 15 and 17, where, between 1857 and 1911, pronounced scouring occurred [fig. 23].

It is reasonable to infer that toxic material precipitated by sea water is carried by the currents and is deposited in the areas of the accumulation of sediment ("fill areas"). According to the report of the Soil Conservation Service, since 1911 the area of most rapid accumulation of silt has migrated further downstream and is now located in the section of Purtan Bay. Thus, sedimentation data provide reasonable explanation for the fact that the poorest oysters are found at some distance from the place of discharge of the pollutant.

The cultivation of oysters in the York River was conducted by the oystermen according to the methods generally employed in Virginia. It consisted in planting seed and growing it to marketable size. As in other sections in the tidewater of Virginia, James River seed was used principally for planting, although there is no doubt that a certain percentage of marketable oysters grew from the local seed. Our observations show that the propagation of oysters in York River has not completely stopped. The setting in the upper part is insignificant but in the lower part it is still of sufficient intensity to produce a set of commercial value. Unfortunately, the mortality among the small oysters in the lower part of the river is very great due to depredation by drills, which in Virginia inflict serious damage to oyster beds located where the salinity of sea water exceeds 15 parts per thousand. In this respect, the York River is no different from Hampton Roads, James River, and other oyster-producing sections of the lower Chesapeake Bay.

A theory has been advanced by representatives of the Chesapeake Corp. (Bailey 1941) that the decline of the oyster industry was "the direct result of poor methods of oyster farming, combined with silting." According to Bailey (loc. cit.) the York River oystermen had tonged most of the oysters and had failed to return to the river any appreciable amount of shells. Because of this practice, the level

of the existing oyster bars was lowered and increased silting of the river covered them with soft mud.

Silting and poor management of oyster reefs is often responsible for the destruction of productive oyster grounds. Examples of such conditions can be found in the depleted natural oyster grounds in South Carolina, Georgia, and Texas. If the failure of the York River oyster industry resulted from a combination of these conditions one would expect to find a gradual decrease in the acreage available for cultivation. We know, however, that the principal difficulty in the York River was the poor quality of oysters, very low yield in pints of shucked oysters per bushel, discoloration of oyster meats, and unpleasant flavor. These conditions are not found on the grounds depleted through overfishing. It is reasonable to expect that they are due to some abnormal condition of the environment and are not the result of mismanagement or defects in the methods of oyster culture.

There is no doubt that because of deforestation and cultivation of land, soil erosion has greatly increased with the corresponding increase in sedimentation of our rivers. The condition is general for the Atlantic coast and is not unique for the York River. We know, however, that oyster grounds in James River continue to produce good oysters and up to the present provide the principal source of seed for Virginia oyster growers. Likewise, there are no signs that oysters in the Piankatank River are abnormal or poor. Observations and experiments described in this report show that the difficulty was confined to the upper part of the York River and that there was a rapid recovery of York River oysters after removal from the polluted waters. Bailey's report fails to mention the peculiar condition of oysters or the fact that the York River receives large quantities of pulp-mill effluents, but blames the oyster industry for its poor practices and lack of conservation. He also states that "the freshets that brought down the silt also caused fluctuations in the salinity of the upper river, and with this change in salinity and silt conditions came new conditions as well as new pests." Some of the pests he mentions, namely, the oyster drill (*Urosalpinx cinerea*) and the starfish (*Asterias forbesi*) are so sensitive to lowered salinity of water that the latter constitutes a barrier protecting the upstream oyster grounds against the depredation by these pests. It is a well established fact that the lowered salinity cannot be responsible for bringing these enemies to the oyster grounds.

In order to demonstrate that low oyster-production is not the result of pollution, the Chesapeake Corp. acquired a large percentage of the leases and put into operation a plan of growing oysters on trays suspended or placed above the bottom. The grounds selected for this purpose are located in the lower part of the river below Claybank wharf and at the mouth of Queens Creek. As shown in the preliminary report (Galtsoff *et al.*, 1938), and in the present paper, these grounds have not been affected by pulp-mill pollution. The results of raising oysters on platforms have not been disclosed by the Chesapeake Corp. in detail with the exception of Mr. Bailey's statement (p. 7, loc. cit.) that "While the primary purpose of the experiment was to demonstrate that an abundance of oysters of high quality could be produced in the York River when planted on hard bottoms or raised above the smothering silt deposits that prevail over a greater portion of the river bottom, the tray project, as carried on by the Chesapeake Corp., is on a practical basis in which money is only invested with the prospect of a fair return." As the method requires a large investment of capital and can be carried out only in the localities well protected against strong wind and waves, it obviously cannot be used by local oystermen lacking large financial support and having leases in the exposed areas of the river and in the bay. Furthermore, the method in which oysters are exposed at low tide is unsuitable for Virginia waters and in other localities where low winter temperature might kill them by freezing. To be applicable to Chesapeake Bay and other waters north, the platform should be placed below low-water level.

During the course of the present studies, the Chesapeake Corp. carried on a parallel investigation of the physiological effect of pulp-mill effluent on oysters. The results of these studies were not described in detail in any technical journal but a brief summary was published in a popular article by May (1943) which appeared in the February 1943 issue of the magazine *Travel*. According to the description given in this article, the Corporation conducted a series of tests in which a number of trays containing 2-year-old oysters were placed at seven stations over a distance of 19 miles along the river, from 1½ miles below West Point to Queens Creek. At each of these stations four trays with 2-year-old

oysters were placed on the bottom and four trays suspended 18 inches above the bottom. The experiment lasted 11 months. How often the trays were examined is not known, but May states (p. 90, loc. cit,) that "these guinea-pig mollusks were watched almost breathlessly by the experimenters."

At the end of the eleventh month it was found that the oysters placed at the four stations located in the areas of greater sedimentation ("fill" areas) showed a "composite" survival of 65 percent in suspended trays and 22 percent survival on the muddy bottom. At the three stations in the "scour" areas the mortality was about the same for both the top and bottom baskets. (Unfortunately, the author fails to disclose the exact figures of mortality.) The investigators of the Chesapeake Corp. draw from these data a conclusion that "the entire test shows that silt caused 40 percent death in the 'fill' areas, against practically no mortality because of silt in the 'scour' area." In the absence of a detailed description of the experiment and because of the omission of essential data showing separately the mortality at each of the stations, it is difficult correctly to evaluate the results of the test. One fact, however, appears to be significant. The reported cumulative mortality of 35 percent of the oysters in the suspended baskets, and of 78 percent of those in bottom baskets, placed in the fill areas, far exceeds the normal annual mortality of the oyster population which, according to our observation, usually does not exceed 10 percent. It is obvious that either the experimental technique was defective or the conditions in York River were deleterious to oysters. Probably the latter assumption is correct; certainly, it is in accord with the findings of this report which have demonstrated the toxic effect of the pulp-mill effluent on the physiology of the oyster. High mortality rate among oysters, reported by the Chesapeake Corp. and not observed by the authors of this report, was probably due to the crowded condition of oysters kept in trays suspended in polluted water, to injuries caused by transplanting them, and in taking up and lowering the trays for inspection, and, possibly, to other factors involved in the experiment. The fact that the death rate was higher among the oysters placed in mud than among those suspended above it is not surprising. Soft mud is not a healthy habitat for oysters. In the York River this environment is even less favorable because the toxic fraction of the black liquor is probably precipitated in part by salt water and is deposited in the areas of the fill.

To prove that pulp-mill effluent has no deleterious effect on oysters the Chesapeake Corp. conducted a survival experiment, the details of which are not disclosed. It is stated, however, by May (p. 30, loc. cit.) that the experiment conducted from November 9, 1938 to May 18, 1939, consisted in keeping oysters in glass tanks filled with water from Piankatank River to which the pulp-mill effluent was added in doses "beginning with the average percentage for York River and increasing up to 77 times. The latter concoction was the color of creamless coffee." Three duplicate tanks with pure sea water were used as controls. It is not stated how often the water was renewed. At the conclusion of the experiment, writes Mr. May, "there was a momentous oyster opening attended by all the important personnel of the mill. There was also present Mr. J. R. Nelson who had spent much of his life in oyster culture who presided as an official observer." Death of one oyster in the control was recorded.

Final conclusion from the experiment conducted by the Chesapeake Corp. is formulated as follows:

> The experiment proved that 77 times the normal percentage would not bring death to a York River bivalve, probably because the carbohydrates or other sugary compounds, the salty compounds such as sodium carbonate and the ordinary vegetable matter in effluent are natural shellfish foods although little of them might reach down river oysters in the widely flowing and rather deep York * * *. In general the more effluent in the test tanks the fatter and happier the oysters appeared.

It is not clear whether this was only a personal conclusion of May or that he expresses a concensus of opinion of all who were present at a "momentous oyster opening." Professional scientists would not venture to ascertain the "happiness" of the oyster and therefore disregarded this part of the conclusion. As to the effect of the pulp-mill effluent on fattening of oysters the results of the experiment, if they are correctly presented, contradict all the observations described in detail in the present report. If May's statement be considered seriously, one would be tempted to infer that increased pulp-mill pollution of water in the York River should be encouraged for it would cause oysters to fatten and make them "happy."

It has been shown in the present study that the specific gravity and toxicity of the pulp-mill effluent were subject to great fluctuations. A certain decrease in toxicity took place after considerable

improvement in the disposal of the effluent was made at the pulp-mill plant. Furthermore, chemical and toxicological studies described in the report showed that the toxicity of the pulp-mill effluent could be greatly reduced by oxidation (p. 164, fig. 68). This suggests a method of treating the effluent which would render it harmless before it is discharged into tidal waters. It is considered, however, that working out a purely technical problem of the process of treatment to be used at the mill is beyond the scope of the present investigation. The data obtained by the authors demonstrate that the physiological effect of the pulp-mill pollutant can be made harmless through oxidation. It must be pointed out, however, that oxidation proceeds rather slowly since the physiological effectiveness of the samples of pulp-mill effluent was destroyed only after vigorous treatment with pure oxygen. One may expect, therefore, that oxidation in the river may be a slow process and that the depressive action of pulp-mill effluent may remain effective for a long time. Experiments with samples of river water collected at West Point (p. 132) corroborate this inference.

The results of several years of intensive study, carried out by the authors and described in detail in this report, have been presented here with the hope that they will be useful to the pulp-mill industry and to State conservation agencies in working out a practical solution to the problem of treatment and safe disposal of pulp-mill wastes. It is the authors' strong belief that the cause of the conservation of our seafood resources in coastal waters can best be served by preventing further inroads from pollution and that through cooperation and mutual understanding of the problems involved a way may be found for the coexistence of the pulp mill and the shellfish industries, both valuable and necessary for the welfare of our Nation.

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TABLE 6.—*Hydrographic data for station 20 in the lower York River off Sandbox*

[Average depth 10.5 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature		Salinity		pH		Phosphorus		Percentage saturation with dissolved oxygen	
					Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
1935				*Meters*	*° C.*	*° C.*	*Parts per thousand*	*Parts per thousand*			*Milligrams per cubic meter*	*Milligrams per cubic meter*		
Dec. 6	10:30 a. m.	4	LE	1.7	6.6	6.5	20.23	20.37	7.9	7.9			94.2	92.2
12	1:45 p. m.	5	½E	1.7	6.7	6.8	20.59	20.84	8.0	8.0			96.2	90.5
23	2:40 p. m.	6	LE	1.7	3.4	3.6	21.53	21.49	7.9	7.9			110.8	96.8
1936														
Jan. 4	9:20 a. m.	7	LE	1.1	1.6	1.6	21.08	21.08	7.9	7.9			95.1	94.1
21	10:25 a. m.	8	FE	1.7	2.4	2.4	11.56	11.60	7.7	7.7	[2] Tr.	Tr.		
Feb. 19	10:35 a. m.	9	LE	.8	.5	.7	13.35	15.68	7.9	7.9	16.0	16.0	94.5	93.9
28	9:55 a. m.	11	FF	1.1	2.6	2.5	14.83	14.96	7.9	7.9	Tr.	Tr.		
Mar. 4	1:50 p. m.	12	½E	1.8	4.9	3.9	12.93	12.39	7.8	7.7	Tr.	Tr.		
16	10:30 a. m.	14	½E	1.3	8.8	7.1	12.88	15.70	8.1	8.1	3.0	Tr.	101.2	104.7
23	3:10 p. m.	16	FE	1.0	8.6	8.3	13.66	13.98			Tr.			
30	3:45 p. m.	17	LF	1.1	12.7	12.1	11.26	12.29	8.2	8.1	Tr.	Tr.	114.4	114.6
Apr. 8	9:10 a. m.	18	HWS	1.0	10.3	10.1	12.70	12.68	8.1	8.1	Tr.	Tr.		
14	9:45 a. m.	20	LE	.8	11.6	11.1	10.28	10.54	8.0	8.0	0	0	99.7	96.5
May 1	9:20 a. m.	21	LE	.7	15.9	15.4	13.01	13.84	8.4	8.4	Tr.	Tr.		
12	9:45 a. m.	22	½F	1.5	19.7	19.2	13.87	14.09	8.3	8.3	Tr.	Tr.		
28	10:30 a. m.	23	½E	1.1	21.5	21.4	15.25				3.0	1.0	94.3	
June 27	9:20 a. m.	28	LE	1.2		22.5		13.89						
30	2:05 p. m.	29	LWS	1.1	25.3	24.9	17.63	18.22	8.3	8.4			106.9	115.5
July 6	1:40 p. m.	29a	½E	1.1	25.5	25.8	18.50				Tr.	Tr.		
15	10:45 a. m.	30	LE	1.1	26.7	26.5	19.96	19.96	7.8	7.8	6.2	6.2		
27	10:30 a. m.	32	LE	1.8	26.4	26.1	21.00	21.08	7.7	7.9	4.0	3.1	110.2	101.1
Aug. 14	12:30 p. m.	33	LE	1.5	27.3	27.0	20.82	20.82	7.9	7.9	6.2	6.2		
26	2:30 p. m.	34	½F	1.8	29.3	28.3	21.92	21.92	8.1	8.1	6.2	6.2	105.3	101.0
Sept. 14	10:15 a. m.	35	HWS	1.5	25.2	25.3	23.39	23.42	7.6	7.7			84.8	88.4
Oct. 2	9:45 a. m.	36	LF	1.5	21.4	21.3	23.64	23.68	7.8	7.9	30.0	24.8	93.8	97.7
20	9:30 a. m.	37	½F	1.7	20.1	20.0	23.40	23.51	8.1	8.1	12.4	12.4	74.2	88.5
Nov. 6	8:45 a. m.	38	LWS	1.9	14.9	14.6	23.13	23.22	8.1	7.8	12.4	12.4	92.0	95.6
24	2:20 p. m.	39	FF	2.0	9.7	9.7	22.94	20.14	8.0	8.1	30.0	18.6		
Dec. 8	10:30 a. m.	40	LWS	1.6	5.1	5.2	22.65	22.66	8.0	8.0	Tr.	Tr.		
14	10:30 a. m.	42	FE		5.7	5.7	21.91	21.96	7.9	7.9	6.2	Tr.		
1937														
Jan. 4	2:25 p. m.	43	LF	2.0	7.7	7.4	21.02	21.13	7.9	7.9	Tr.	Tr.		
25	2:30 p. m.	45	LE	1.8	10.5	10.1	16.82	17.14	8.1	8.1	Tr.	Tr.	99.6	95.4
Feb. 15	10:50 a. m.	46	HWS	1.2	5.5	5.5	18.37	18.57	7.8	7.9				
Mar. 5	9:45 a. m.	47	LWS	1.9	4.4	4.2	16.83	17.48	8.1	8.1	15.0	20.0	101.8	94.8
31	9:45 a. m.	49	LF	.7	7.7	7.7	17.21	17.21	8.4	8.4	Tr.	Tr.	105.5	104.0
Apr. 26	3:35 p. m.	50	LE	1.0	13.6	13.3	18.30	18.57	8.1	8.1	6.2	6.2	96.8	90.7

[1] LWS=Low water slack; HWS=High water slack; LE=Last of ebb; LF=Last of flood; FF=First of flood; etc.
[2] Tr.=Trace.

TABLE 7.—*Hydrographic data for station 14 in the York River below Carmines Islands*

[Average depth 8.3 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature		Salinity		pH		Phosphorus		Percentage saturation with dissolved oxygen	
					Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
1935				*Meters*	*° C.*	*° C.*	*Parts per thousand*	*Parts per thousand*			*Milligrams per cubic meter*	*Milligrams per cubic meter*		
Dec. 2	10:30 a. m.	4	LE		9.3	9.2	20.63	20.46	7.7	7.7			92.5	93.0
12	12:45 p. m.	5	FE	1.2	6.4	6.6	20.26	20.30	8.0	8.0			95.8	96.4
1936														
Jan. 3	2:40 p. m.	7	FF	.7	2.4	2.2	20.70	20.77	8.0	8.0			96.8	97.4
21	12:10 p. m.	8	LE	1.0	3.2	3.2	13.12	13.57	7.7	7.7	[2] Tr.	Tr.		
Feb. 19	12:50 p. m.	9	LWS	.7		.7		10.03		7.7		12.4		93.4
27	4:00 p. m.	11	½E		3.8	3.6	13.44	13.30	7.9	7.9	Tr.		96.6	85.6
Mar. 4	3:15 p. m.	12	LE	1.3	6.2	6.1	10.23	10.32	7.7	7.7	Tr.	Tr.		
18	11:45 a. m.	14	FE	1.2	8.7	8.4	13.68	14.76	8.1	8.1			103.5	109.0
24	8:50 a. m.	16	½F	.6	8.8	8.5	16.22	12.52	7.9	8.0	Tr.	Tr.		
Apr. 8	11:45 a. m.	18	FF	.7	10.5	10.4	12.16	12.09	7.9	7.9	Tr.	Tr.		
14	10:45 a. m.	20	LWS	.7	12.3	11.9	7.83	9.54	7.8	8.0	0	0	92.3	100.0
27	10:00 a. m.	21	FF	.7		12.7		14.16		8.6		Tr.		117.5
May 12	10:50 a. m.	22	LF	1.1	21.1	20.1	12.77	13.78	8.2	8.2	Tr.	Tr.		
28	1:20 p. m.	23	FF	.7		22.9		15.26				Tr.		

[1] LWS=Low water slack; HWS=High water slack; LE=Last of ebb; LF=Last of flood; FF=First of flood; etc.
[2] Tr.=Trace.

TABLE 7.—*Hydrographic data for station 14 in the York River below Carmines Islands*—Continued

Date	Time	Cruise	Tide [1]	Turbidity-disc reading	Water temperature		Salinity		pH		Phosphorus		Percentage saturation with dissolved oxygen	
					Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
				Meters	*° C.*	*° C.*	*Parts per thousand*	*Parts per thousand*			*Milligrams per cubic meter*	*Milligrams per cubic meter*		
1936														
June 8	3:45 p. m.	24	½E	1.0		22.9		17.18		8.3				
11	2:00 p. m.	25	FF		23.4	22.8								
19	2:15 p. m.	26	½E	.9		24.8		17.36		8.0				
25	2:40 p. m.	27	HWS	1.2	22.7	22.7	17.61	17.72	7.5	7.7				
26	9:05 a. m.	28	LE	.8	21.9	21.9		17.56		7.7				
30	12:10 p. m.	29	LWS	.9		25.8		17 07		7.9		[2] Tr.		100.3
July 8	9:30 a. m.	30	FF	.8	25.2	24.9								
15	2:45 p. m.	31	½F	.7	27.9	27.9		19.43			6.2	6.2		
27	2:00 p. m.	32	FF	.8	27.3	27.3	20.35	20.44	7.9	7.9	3.1	3.1	109.2	107.6
Aug 14	10:30 a. m.	33	LE	1.8		28.0		20.68		7.9		6.2		
26	12:15 p. m.	34	LW	1.5	29.0	28.7	21.02	21.29	7.8	7.8	6.2	6.2	86.8	87.4
Sept. 9	2:15 p. m.	35	½F	1.1		25.6		22.34		7.5		3.1		101.1
29	9:40 a. m.	36	HWS	1.1	22.5	22.6	23.51	23.51	8.0	7.8	6.2	18.6	83.3	82.1
Oct. 20	2:45 p. m.	37a	½E	1.3	20.0	20.0	22.68	22.74	8.1	8.0	12.4	12.4	115.5	120.2
27	8:45 a. m.	37	FE		17.6	17.0					12.4			
Nov. 5	9:15 a. m.	38	FF			15.8		22.50		7.7		12.4		92.5
24	12:45 p. m.	39	FF	1.7		9.0		22.23		8.1		18.6		
Dec. 3	10:40 a. m.	40	LF	1.4	6.1	4.3	22.56	22.45	7.9	7.9	12.4	12.4		
14	12:30 p. m.	42	½E	1.8	5.8	5.8	21.67	21.92	7.7	7.9	6.2	12.4		
1937														
Jan.	2:15 p. m.	43	LF	1.6		7.2		18.95		7.9		Tr.		
26	1:00 p. m.	45	FE	1.1		9.6		7.91		7.6		Tr.		87.9
Feb. 12	9:00 a. m.	46	LF	.6	4.8	4.7	16.91	16.83	7.8	7.7				
Mar. 4	11:45 a. m.	47	FF	.7	5.2	5.3	14.99	15.03	8.0	8.2	20.0	20.0	91.7	92.4
22	10:25 a. m.	48	E			7.5		15.61				3.1		
31	11:00 a. m.	49	LF	1.0	8.0	8.1	16.60	16.55	8.4	8.4	Tr.	Tr.	105.4	107.2
Apr. 23	11:45 a. m.	50	FE	1.0	15.4	15.2	16.28	16.38	8.3	8.1	6.2	6.2	100.2	102.1
June 16	5:00 p. m.	51	FF			24.9		17.86				6.2		

[1] LWS=Low water slack; HWS=High water slack; LE=Last of ebb; LF=Last of flood; FF=First of flood; etc.
[2] Tr.=Trace.

TABLE 8.—*Hydrographic data for station 15 in the York River just above Queens Creek*

[Average depth 3.4 feet]

Date	Time	Cruise	Tide [1]	Turbidity-disc reading	Water temperature	Salinity	pH	Phosphorus	Percentage saturation with dissolved oxygen
				Meters	*° C*	*Parts per thousand*		*Milligrams per cubic meter*	
1935									
Dec. 2	12:20 p. m.	4	FF	0.5	8.7	18.66	7.7		103.2
12	11:40 a. m.	5	HWS	.6	6.5	18.42	7.9		109.0
1936									
Jan. 3	1:35 p. m.	7	FF	.6	3.0	18.80	8.0		97.6
21	1:45 p. m.	8	LE	.4	2.9	8.60	7.5	[2] Tr.	
Feb. 19	2:05 p. m.	9	FF	.2	2.0	5.93	7.7		90.8
Mar. 5	9:25 a. m.	12	FE	.8	3.2	12.70	7.7	Tr.	
16	2:15 p. m.	14	FF	.8	10.7	8.48	8.2	Tr.	104.7
24	10:10 a. m.	16	½F	.6	9.4	10.30	8.0	Tr.	
30	10:35 a. m.	17	FF	.8	12.4	8.96	7.8	Tr.	108.9
Apr. 8	2:45 p. m.	18	LE	.2	11.3	6.35	7.5	Tr.	
14	11:45 a. m.	20	FF	.2	13.6	7.83	8.2	0	94.9
27	11:00 a. m.	21	FF	.1	13.9	11.74	8.1	Tr.	95.2
May 12	11:45 a. m.	22	LF	.5	21.6	12.63	8.0	Tr.	
28	11:00 a. m.	23	½F	.3	22.9	13.53		Tr.	101.1
June 11	1:15 p. m.	25	FF		25.4				
26	10:45 a. m.	28	FF	.6	21.8	15.55	7.6		
30	11:15 a. m.	29	LE	.5	25.7	16.49	7.7	Tr.	104.0
July 8	10:30 a. m.	30	FF	.4	25.8				
16	9:45 a. m.	31	½E	.7	27.6	18.71	7.5	6.2	
27	3:00 p. m.	32	½F		28.4	18.75	7.9	3.1	108.3
Aug. 14	9:30 a. m.	33	LE	1.0	27.0	19.63	7.7	12.4	
26	10:30 a. m.	34	LWS	.3	28.8	19.85	7.7	6.2	82.0
Sept. 9	2:40 p. m.	35	LF	.7	27.1	20.88	7.7	6.2	106.0
29	11:30 a. m.	36	FE	.3	22.7	22.23	7.7	12.4	88.0
Oct. 20	4:00 p. m.	37	LE	.5	19.9	22.03	7.7	18.6	83.0
Nov. 5	1:45 p. m.	38	LF	.2	15.4	20.63	7.7	12.4	93.7
24	11:45 a. m.	39	LE	1.1	8.4	20.14	8.1	18.6	
Dec. 3	11:35 a. m.	40	LF	.6	5.9	20.44	7.9	6.2	
14	1:00 p. m.	42	½E	.6	5.7	20.19	7.7	6.2	
1937									
Jan. 6	3:15 p. m.	43	LF	.5	7.0	15.97	8.1	Tr.	
26	12:10 p. m.	45	FE	.6	9.7	11.83	7.6	Tr.	90.8
Feb. 12	9:30 a. m.	46	LF	.3	5.0	16.00	7.7		
Mar. 4	12:45 a. m.	47	FF	.7	6.2	14.60	8.1	20.0	98.1
22	2:00 p. m.	48	FF		9.6	12.34		6.2	
31	12:00 m.	49	LF	.6	8.4	12.67		Tr.	103.9
Apr. 23	12:30 p. m.	50	½E	.4	17.3	14.94	8.1	6.2	111.8

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, LF=Last of flood, FF=First of flood, etc.
[2] Tr.=Trace.

TABLE 9.—*Hydrographic data for station 23 in the York River above Claybank*

[Average depth 4.6 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature	Salinity	pH	Phosphorus	Percentage saturation with dissolved oxygen
				Meters	*° C.*	*Parts per thousand*		*Milligrams per cubic meter*	
1936									
June 26	11:05 a. m.	28	FF	0.5	22.9	14.40	7.5		
July 8	11:40 a. m.	30	½F	.5	26.1				
16	10:30 a. m.	31	FE	.6	27.3	18.44	7.6		
29	10:50 a. m.	32	LWS	.5	28.1	17.11		3.1	91.5
Aug. 13	10:15 a. m.	33	½E	.8	26.9	18.01	7.9	12.4	
31	2:20 p. m.	34	LE	.9	26.3	19.16	7.7	12.4	92.8
Sept. 9	3:15 p. m.	35	LF	.8	25.3	20.41	7.6	6.2	90.6
29	12:40 p. m.	36	FE	.3	22.7	21.71		6.2	82.9
Oct. 21	10:00 a. m.	37	FF	1.0	19.4	20.01	7.8	12.4	91.2
Nov. 5	10:45 a. m.	38	FF	.5	15.6	20.72	7.7	12.4	91.0
24	11:10 a. m.	39	½E	1.1	8.1	19.79	7.9	18.6	
Dec. 3	12:30 p. m.	40	LF	.9	6.0	20.88	7.7	12.4	
14	1:40 p. m.	42	½E	1.1	5.8	21.55	7.9	6.2	
1937									
Jan. 6	4:00 p. m.	43	LF	1.2	7.2	16.18	7.8	[2] Tr.	
26	11:30 a. m.	45	FE	.7	9.6	12.54	7.6		89.1
Feb. 12	10:10 a. m.	46	LF	.3	4.7	14.13	7.6		
Mar. 4	1:15 p. m.	47	½F	.4	5.9	9.94	7.9	15.0	96.3
31	12:45 p. m.	49	LF	.8	8.3	15.12	8.3		106.7
Apr. 23	1:10 p. m.	50	½E	.5	16.4	12.95	8.3	6.2	107.3
June 7	12:00 m.	51	½E		26.8				

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, LF=Last of flood, FF=First of flood, etc.
[2] Tr.=Trace.

TABLE 10.—*Hydrographic data for station 5 in the middle York River just above Allmonds Wharf*

[Average depth 3.9 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature	Salinity	pH	Phosphorus	Percentage saturation with dissolved oxygen
				Meters	*° C.*	*Parts per thousand*		*Milligrams per cubic meter*	
1935									
Oct. 17	2:30 p. m.	1	LF		17.9	18.28			
Nov. 11	1:20 p. m.	2	FE		16.8	17.21			
Dec 6	1:35 p. m.	4	LE	0.5	5.8	14.96	7.8		91.7
12	10:40 a. m.	5	LF	.6	6.2	16.51	7.8		88.6
1936									
Jan 3	12:35 p. m.	7	FF	.6	1.2	17.63	7.9		94.1
23	12:15 p. m.	8	FE		.9	7.79	7.4		
Feb. 20	10:30 a. m.	9	½E	.8	.3	8.98	7.6		95.0
27	2:35 p. m.	11	FE	.9	4.2	8.47	7.3	[2] Tr.	93.5
Mar. 5	10:30 a. m.	12	FE	.7	7.0	6.93	7.5	Tr.	
18	2:10 p. m.	14	LE	.4	11.2	7.29	7.9		101.1
24	11:15 a. m.	16	LF	.6	10.6	5.81	7.8	Tr.	
30	11:50 a. m.	17	FF	.4	13.2	3.80	7.5	Tr.	90.7
Apr. 8	3:30 p. m.	18	LE			6.64	7.5	Tr.	
14	1:00 p. m.	20	FF	.4	13.8	5.64	7.6	0	89.1
27	1:00 p. m.	21	LF	.6	15.2	9.54	8.1	Tr.	113.8
May 12	12:45 p. m.	22	HWS	.3	22.6	10.64	7.6	Tr.	
June 1	11:40 a. m.	23	½E	.2	21.6	11.35		3.0	107.0
8	2:15 p. m.	24	FE	.3	23.0		7.8		
11	12:00 m.	25	FF		26.0				
26	11:25 a. m.	28	FF	.5	22.9	13.89	7.5		
30	10:20 a. m.	29	½E	.3	25.2	13.31	7.7	Tr.	91.8
July 8	12:30 p. m.	30	LF	.4	26.3				
16	10:50 a. m.	31	FE	.5	27.9	17.32	7.5	6.2	
29	12:00 m.	32	FF	.5	28.1	16.33		3.1	90.6
Aug. 13	2:45 p. m.	33	LE	.8	28.6	16.58	7.9	6.2	
30	12:00 m.	34	LE	.4	26.0	18.08	7.7	12.4	88.2
Sept. 10	11:15 a. m.	35	LE	.8	25.3	18.98	7.7	6.2	96.5
29	1:15 p. m.	36	½E	.7	22.7	21.11	7.9	6.2	88.2
Oct. 21	10:45 a. m.	37	FF	1.2	18.6	19.24	7.9	18.6	104.8
Nov. 5	1:00 p. m.	38	LF	.5	15.4	19.04	7.9	18.6	102.8
24	10:00 a. m.	39	FE	.4	8.4	19.18	7.9	18.6	
Dec. 3	1:00 p. m.	40	HWS	.3	5.7	19.98	7.7	12.4	
14	2:10 p. m.	42	½E	1.0	5.8	18.78	7.7	6.2	
1937									
Jan. 8	3:45 p. m.	43	FF	.7	8.9	9.38	7.8	Tr.	
26	11:15 a. m.	45	FE	.6	9.9	7.88	7.4	Tr.	87.3
Feb. 12	10:45 a. m.	46	LE		4.3	13.57	7.7		
Mar. 4	1:45 p. m.	47	½F	.5	7.2	10.86	7.9	5.0	96.0
22	11:45 a. m.	48	LE		8.2	11.44		3.1	
30	10:20 a. m.	49	LF	.3	8.4	12.47	8.3	Tr.	99.4
Apr. 23	1:30 p. m.	50	½E	.6	17.0	12.39	8.3	6.2	105.9
June 7	2:00 p. m.	50a	LE		29.2			12.4	
16	2:15 p. m.	51	½E		26.7	13.17			

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, LF=Last of flood, FF=First of flood, etc.
[2] Tr.=Trace.

TABLE 11.—*Hydrographic data for station 22 in the York River inside Purtan Bay*

[Average depth 4.1 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature	Salinity	pH	Phorphorus	Percentage saturation with dissolved oxygen
				Meters	*° C.*	*Parts per thousand*		*Milligrams per cubic meter*	
1936									
Apr. 8	3:45 p. m.	18	LE	0.2	10.8		7.6		
30	3:55 p. m.	21	FF	.4	19.9	7.70	8.1		
June 19	12:30 p. m.	26	FE	.4	24.9	13.87	7.7		
July 8	1:15 p. m.	30	FF	.3	26.8				
16	11:30 a. m.	31	½E	.5	28.3	16.35	7.7		
29	1:45 p. m.	32	FF	.3	28.5	16.53	7.7	3.1	90.3
Aug. 13	11:30 a. m.	33	LE	.6	27.8	17.27	7.8	8.1	
31	1:25 p. m.	34	LE	.7	26.4	18.26	7.9	12.4	106.0
Sept. 10	11:35 a. m.	35	LE	.7	25.4	18.89	7.7	6.2	98.3
Oct. 1	3:45 p. m.	36	½E	.4	22.3	21.22	7.7	62.0	84.0
21	11:10 a. m.	37	FF		19.3	19.29	7.9	30.0	96.8
Nov. 5	12:45 p. m.	38	LF	.3	15.3	19.89	7.7	18.6	93.2
24	10:15 a. m.	39	FE	.4	8.4	18.91	7.9	18.6	
Dec. 4	4:35 p. m.	40	½E	.4	6.2	19.45	7.7	12.4	
14	2:30 p. m.	42	½E	.6	5.8	19.61	7.9	6.2	
1937									
Jan. 8	3:25 p. m.	43	LWS	.6	8.6	8.55	7.8	[2] Tr.	
26	10:45 a. m.	45	HWS	.5	10.0	7.68	7.3	Tr.	85.5
Feb. 12	11:00 a. m.	46	HWS	.3	3.9	13.41	7.6		
Mar. 4	2:00 p. m.	47	LF	.4	6.4	9.33	7.8	15.0	94.8
22	12:30 p. m.	48	LE		9.3	11.09		3.1	
30	10:35 a. m.	49	LF	.6	8.4	12.16	8.3	Tr.	100.0
Apr. 23	1:45 p. m.	50	½E	.6	16.5	12.11	8.3	6.2	112.3
June 7	2:15 p. m.	50a	LWS		28.4				

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, LF=Last of flood, FF=First of flood, etc.
[2] Tr.=Trace.

TABLE 12.—*Hydrographic data for station 6 in the York River just below Taskinas Creek*

[Average depth 5.2 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature	Salinity	pH	Phosphorus	Percentage saturation with dissolved oxygen
				Meters	*° C.*	*Parts per thousand*		*Milligrams per cubic meter*	
1936									
June 19	12:00 m.	26	LF	0.4	24.8	14.72	7.8		
26	12:00 m.	28	FF	.3	22.6	12.56	7.7		
July 10	1:15 p. m.	30	½F	.2	27.7				
16	12:15 p. m.	31	FE	.2	28.8	15.81	7.4		
29	12:50 p. m.	32	FF	.4	28.3	15.61	7.8	6.2	87.6
Aug. 13	2:30 p. m.	33	LE	.5	28.5	16.06	7.8	6.2	
Sept. 10	1:15 p. m.	35	FF	.6	26.0	17.41	7.7	6.2	115.1
Oct. 1	10:15 a. m.	36	HWS	.4	21.6	22.45	7.9	6.2	93.5
21	11:30 a. m.	37	FF	.6	18.2	19.24	7.9	12.4	97.4
Nov. 5	11:20 a. m.	38	FF	.1	14.8	17.83	7.6	18.6	96.3
24	10:40 a. m.	39	FE	.3	8.3	18.30	7.9		
Dec. 4	4:00 p. m.	40	FE	.3	5.6	18.93	7.7		
23	11:40 a. m.	42	LE	.3		12.72	7.7	[2] Tr.	
1937									
Jan. 8	3:00 p. m.	43	LE	.4	8.2	8.12	7.8	Tr.	
26	10:15 a. m.	45	HWS	.5	9.9	6.96	7.4	Tr.	86.4
Feb. 11	2:15 p. m.	46	½E	.2	4.6	9.85	7.4	3.2	
Mar. 4	2:20 p. m.	47	LF	.3	6.2	10.30	7.7	10.0	93.1
30	11:00 a. m.	49	LF	.2	8.1	10.52	8.3	3.1	91.3
Apr. 23	2:20 p. m.	50	LE	.3	17.4	9.60	8.1	6.2	99.2

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, LF=Last of flood, FF=First of flood, etc.
[2] Tr.=Trace.

TABLE 13.—*Hydrographic data for station 16 in the York River off Roanes Point*

[Average depth 4.2 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature	Salinity	pH	Phosphorus	Percentage saturation with dissolved oxygen
				Meters	*° C.*	*Parts per thousand*		*Milligrams per cubic meter*	
1935									
Dec. 6	2:45 p. m.	4	LE	0.5	6.4	12.11	7.7	----------	98.9
13	12:25 p. m.	5	LF	.3	6.6	16.60	7.8	----------	80.5
1936									
Jan. 7	12:00 m.	7	FE	.4	2.0	7.34	7.7	----------	95.3
23	11:20 a. m.	8	FE	----------	1.6	5.97	7.2	----------	----------
Feb. 21	11:10 a. m.	9	FE	.3	0.2	6.19	7.4	[2] Tr.	88.3
Mar. 5	12:45 p. m.	12	LE	.3	5.3	6.29	7.3	Tr.	----------
18	3:25 p. m.	14	LWS	.3	11.1	----------	7.2	----------	100.6
24	12:45 p. m.	16	FE	.6	11.1	3.53	7.3	Tr.	----------
30	12:50 p. m.	17	FF	.6	14.5	1.96	7.3	Tr.	90.1
Apr. 9	10:20 a. m.	18	½F	.3	11.4	3.51	7.4	----------	----------
16	12:00 m.	20	LE	.2	15.7	3.21	7.5	Tr.	92.6
29	11:05 a. m.	21	LWS	.3	18.0	5.41	7.8	Tr.	95.1
May 14	10:45 a. m.	22	½E	.3	20.8	7.30	7.4	Tr.	----------
June 1	12:30 p. m.	23	LE	.5	22.5	10.41	----------	Tr.	101.7
19	11:15 a. m.	25	½F	.3	25.6	13.10	7.6	Tr.	----------
25	1:30 p. m.	26	LE	.4	25.7	12.67	----------	----------	----------
26	12:20 p. m.	28	FF	.6	23.3	11.82	7.5	----------	----------
30	1:15 p. m.	29	½E	.3	25.9	13.06	7.4	Tr.	76.0
July 17	2:30 p. m.	31	FE	.3	29.0	14.79	7.3	3.1	----------
31	11:50 a. m.	32	FE	.3	25.5	17.32	7.5	6.2	66.9
Aug. 13	1:30 p. m.	33	LE	.5	28.3	14.89	7.9	12.4	----------
28	10:45 a. m.	34	FE	.7	27.0	17.81	7.7	12.4	85.0
Sept. 10	12:20 p. m.	35	LE	.5	25.8	16.46	7.6	6.2	96.1
Oct. 1	10:40 a. m.	36	HWS	.5	21.9	20.91	7.8	12.4	69.8
21	12:50 p. m.	37	LF	.5	20.0	17.55	7.8	12.4	92.5
Nov. 4	1:15 p. m.	38	FF	.1	15.8	18.15	7.7	3.1	83.3
19	4:35 p. m.	39	FE	.7	8.3	17.20	7.7	----------	----------
Dec. 4	3:30 p. m.	40	½F	.3	5.6	18.33	7.7	18.6	----------
Dec. 13	11:30 a. m.	42	LE	.4	3.9	12.43	7.7	Tr.	----------
1937									
Jan. 8	2:05 p. m.	43	LE	.4	8.1	6.51	7.6	Tr.	----------
27	10:30 a. m.	45	LF	.3	9.1	5.88	----------	93.0	83.6
Feb. 11	1:30 p. m.	46	FE	.3	5.2	10.77	7.5	----------	----------
Mar. 3	3:35 p. m.	47	LF	.2	5.4	9.80	7.9	6.2	84.2
22	1:00 p. m.	48	LWS	----------	10.2	8.35	----------	----------	----------
30	11:20 a. m.	49	LF	.4	9.0	11.35	8.5	Tr.	98.5
Apr. 27	12:20 p. m.	50	LF	.4	15.5	9.65	7.6	3.2	90.9
June 16	12:30 p. m.	51	LWS	----------	26.4	10.05	----------	12.4	----------

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, FE=First of ebb, FF=First of flood, etc.
[2] Tr.=Trace.

TABLE 14.—*Hydrographic data for station 17 in the York River off Ware Creek*

[Average depth 3.9 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature	Salinity	pH	Phosphorus	Percentage saturation with dissolved oxygen
				Meters	*° C.*	*Parts per thousand*		*Milligrams per cubic meter*	
1935									
Dec. 6	3:15 p. m.	4	LWS	0.4	6.2	11.67	7.7		97.5
1936									
Jan. 7	11:40 a. m.	7	FE	.6	2.2	7.72	7.7		87.7
23	10:30 a. m.	8a	HWS		0.6	3.87	7.2		
Feb. 21	10:30 a. m.	9	HWS	.5	.1	6.91	7.4		
Mar. 6	1:45 p. m.	12	FE	.2	5.9	5.21	7.2	7.0	
19	11:30 a. m.	14	½E		10.3	3.75	7.6	3.0	73.8
25	10:25 a. m.	16	½F	.1	11.3	2.61	7.3	[2] Tr.	
Apr. 1	10:00 a. m.	17	½E	.1	13.2	2.86	7.5	Tr.	82.3
9	10:40 a. m.	18	½F	.3	11.2	4.29	7.4		
16	3:30 p. m.	20	FF	.2	15.2	3.04	7.4	Tr.	100.8
29	11:45 a. m.	21	FF	.1	18.2	6.31	7.9	Tr.	108.3
May 14	10:55 a. m.	22	½E	.0	21.0	6.55	7.4	Tr.	
June 1	1:30 p. m.	23	LE	.2	22.6	11.40		Tr.	109.4
11	11:00 a. m.	25	FF		25.0				
19	10:45 a. m.	26	½F	.4	25.0	12.86	7.6		
July 2	12:30 p. m.	29	½E	.1	25.6	13.21	7.4	Tr.	84.5
17	2:20 p. m.	31	FE	.2	29.1	14.90	7.4	3.1	
31	12:10 p. m.	32	FE	.3	25.3	15.95	7.5	3.1	77.9
Aug. 17	2:10 p. m.	33	FE	.3	28.1	15.97	7.7	30.0	102.6
28	11:30 a. m.	34	LE	.5	26.9	16.62	7.8	6.2	89.8
Sept. 10	12:45 p. m.	35	LE	.4	25.8	15.97	7.7	6.2	100.5
Oct. 1	11:10 a. m.	36	FF	.5	22.0	20.81	7.8	6.2	96.6
21	1:10 p. m.	37	LF	.3	22.0	15.90	7.8	12.4	84.3
Nov. 4	12:45 p. m.	38	FF	.1	15.6	17.48	7.7	3.1	88.2
19	4:20 p. m.	39	FE	.3	8.4	16.89	7.6		
Dec. 4	2:50 p. m.	40	½F	.4	5.7	17.56	7.7	24.8	
23	11:20 a. m.	42	½E	.1	4.3	12.88	7.7	Tr.	
1937									
Jan. 8	1:45 p. m.	43	LE	.4	7.6	7.07	7.7	Tr.	
27	10:50 a. m.	45	LF	.2	9.3	4.65	7.4	93.0	84.7
Feb. 11	1:15 p. m.	46	FE	.2	5.3	10.57	7.3		
Mar. 3	3:10 p. m.	47	½F	.2	5.4	8.31	7.6	6.0	88.2
30	12:05 p. m.	49	LF	.3	8.4			Tr.	
Apr. 27	12:40 p. m.	50	LF	.5	15.0	9.06	7.3	3.1	107.9

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, FE=First of ebb, FF=First of flood, etc.
[2] Tr.=Trace.

TABLE 15.—*Hydrographic data for station 8 in the upper York River inshore of Bell Rock Lighthouse*

[Average depth 13.6 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature		Salinity		pH		Phosphorus		Percentage saturation with dissolved oxygen	
					Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
				Meters	*° C.*	*° C.*	*Parts per thousand*	*Parts per thousand*			*Milligrams per cubic meter*	*Milligrams per cubic meter*		
1936														
Apr. 29	12:25 p. m.	21	FF	0.2	15.9	15.3	3.69	4.43	7.3	7.3			86.1	82.0
June 26	12:50 p. m.	28	FF	.6		23.9		12.92		7.5				
July 10	12:00 m.	30	FF	.3		27.7								
17	2:00 p. m.	31	FE	.3		29.1		14.22		7.5				
31	12:50 p. m.	32	½E	.3		26.0		16.02				3.2		78.2
Aug. 17	2:00 p. m.	33	FE	.3		27.8		13.33		7.9				99.8
Sept. 11	11:50 a. m.	35	½E	.4		26.2		16.96		7.7		6.2		101.1
Oct. 1	1:00 p. m.	36	FE	.5		21.7		20.73		7.7		6.2		83.3
22	11:00 a. m.	37	FF	.5	19.2	19.3		19.24		7.9		12.4	81.4	65.0
Nov. 4	12:00 m.	38	FF	.7	15.7	15.6		17.83		7.6		3.1	85.5	82.9
19	4:10 p. m.	39	FE	.7	8.5	8.6	17.03	18.03	7.5	7.7				
Dec. 4	2:30 p. m.	40	FF	.4	5.3	5.2	17.65	17.54	7.7	7.7	12.4	18.6		
23	11:05 p. m.	42	½E	.8	4.2	4.3	11.31	12.03	7.7	7.7	[2] Tr.	Tr.		
1937														
Jan. 8	12:30 p. m.	43	LE	.4	7.0	7.1	5.73	11.60	7.6	7.7	Tr.	Tr.		
27	11:20 a. m.	45	LF	.3	9.0	9.3	5.12	6.35	7.2	7.2	93.0	93.0	84.7	81.1
Feb. 11	12:45 p. m.	46	FE	.4	5.6	4.9	13.55	14.05	7.6	7.6	Tr.	Tr.		
Mar. 3	2:00 p. m.	47	FF	.4	5.4	4.6	7.11	7.85	7.5	7.5	8.0		85.1	83.8
30	12:40 p. m.	49	LF	.4	8.9	8.5					Tr.	Tr.		
Apr. 27	12:55 p. m.	50	LF	.6	15.6	14.3	8.17	9.78			3.1	3.1	87.3	81.7

[1] LWS=Low water slack; HWS=High water slack; LE=Last of ebb; LF=Last of flood; FF=First of flood; etc.
[2] Tr.=Trace.

TABLE 16.—*Hydrographic data for station 9 in the upper York River on the middle ground just below West Point*

[Average depth 12.4 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature		Salinity		pH		Phosphorus		Percentage saturation with dissolved oxygen	
					Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
				Meters	*° C.*	*° C.*	*Parts per thousand*	*Parts per thousand*			*Milligrams per cubic meter*	*Milligrams per cubic meter*		
1935														
Oct. 22	10:20 a. m.	P2	FE	--------	19.1	18.0	9.89	12.61	--------	--------	--------	--------	--------	--------
29	8:55 a. m.	P3	FF	--------	16.9	16.6	11.13	13.02	--------	--------	--------	--------	--------	--------
Nov. 8	9:15 a. m.	2	LF	--------	16.4	16.4	14.34	14.47	--------	--------	--------	--------	--------	--------
Dec. 3	3:50 p. m.	4	½E	0.7	8.1	8.2	11.53	13.89	7.6	7.5	--------	--------	--------	--------
13	11:30 a. m.	5	½F	.5	6.4	6.3	13.04	13.04	7.7	7.7	--------	--------	89.0	89.7
1936														
Jan. 7	10:45 a. m.	7	HWS	.4	1.9	1.8	3.87	8.62	7.4	7.6	--------	--------	88.8	90.3
22	12:45 p. m.	8	½E	.4	3.2	3.0	5.01	8.13	7.4	7.5	--------	--------	--------	--------
Feb. 20	2:05 p. m.	9	LE	.2	.4	0.3	1.96	7.83	7.1	7.3	--------	--------	87.9	86.0
27	12:15 p. m.	11	HWS	.3	2.9	2.7	0.86	2.30	6.9	7.1	[2] Tr.	Tr.	85.2	72.3
Mar. 5	2:00 p. m.	12	LE	.3	5.2	4.8	3.35	5.55	7.2	7.3	Tr.	Tr.	--------	--------
19	12:00 m.	14	½E	--------	10.8	10.9	1.21	3.95	7.3	7.3	8.0	Tr.	80.2	86.2
25	11:00 a. m.	16	½F	.2	11.2	11.3	1.64	1.42	7.2	7.3	Tr.	Tr.	--------	--------
Apr. 1	10:45 a. m.	17	½E	.2	12.2	12.9	2.54	5.01	7.1	7.3	Tr.	Tr.	76.7	80.3
9	11:15 a. m.	18	½F	.2	11.7	11.7	--------	2.11	7.2	7.3	6.2	Tr.	--------	--------
16	1:00 p. m.	20	LWS	.2	13.2	13.2	.39	2.50	7.1	7.4	12.4	Tr.	94.3	106.8
29	1:40 p. m.	21	FF	.2	16.3	15.6	2.02	2.88	7.1	7.3	6.2	6.2	85.2	83.9
May 14	11:30 a. m.	22	½E	.3	21.7	21.6	4.51	5.73	7.3	7.3	Tr.	0	--------	--------
June 3	11:45 a. m.	23	LF	.5	23.1	22.8	10.72	10.73	--------	--------	3.0	2.0	114.9	108.7
8	12:00 m.	24	LF	.5	23.1	23.2	11.98	11.49	7.9	7.9	--------	--------	--------	--------
16	12:15 p. m.	25	½E	.6	24.8	24.2	11.24	12.30	--------	--------	Tr.	0	--------	--------
19	10:10 a. m.	26	½F	--------	24.8	24.8	11.55	11.78	7.5	7.5	--------	--------	--------	--------
26	1:30 p. m.	28	FF	.6	23.1	--------	18.15	--------	7.4	--------	--------	--------	--------	--------
July 2	11:45 a. m.	29	½E	.6	25.2	24.6	11.78	14.09	7.6	7.4	13.0	Tr.	97.1	87.1
10	11:00 a. m.	30	FF	.6	28.3	27.2	--------	--------	--------	--------	--------	--------	--------	--------
17	1:30 p. m.	31	FE	.8	29.9	28.2	13.35	12.94	7.4	7.5	6.2	12.4	--------	--------
31	1:15 p. m.	32	½E	.6	26.3	26.1	13.77	16.28	--------	--------	6.2	3.2	83.4	57.2
Aug. 17	1:00 p. m.	33	LF	.5	27.7	27.5	14.33	14.49	7.9	7.8	30.0	12.4	96.7	89.1
28	12:30 p. m.	34	LE	.8	28.0	27.9	15.90	17.11	7.5	7.5	12.4	6.2	59.0	62.3
Sept. 11	12:30 p. m.	35	LE	.5	26.0	25.9	15.44	16.49	7.7	7.7	3.1	3.1	90.2	87.3
Oct. 1	1:30 p. m.	36	FE	.4	21.7	21.5	18.93	18.86	7.8	7.8	6.2	6.2	86.6	91.7
22	11:45 a. m.	37	FF	--------	20.2	19.6	14.65	14.11	7.8	7.8	12.4	12.4	83.6	81.6
Nov. 4	11:30 a. m.	38	LWS	.6	15.7	15.6	14.52	15.23	7.4	7.5	3.1	3.1	81.4	76.8
19	3:40 p. m.	39	HWS	.6	8.7	8.7	17.07	17.09	7.6	7.7	--------	--------	--------	--------
Dec. 4	1:30 p. m.	40	FF	.6	5.4	5.2	15.81	15.99	7.7	7.7	30.0	12.4	--------	--------
15	3:35 p. m.	42	½E	1.0	5.0	5.0	14.76	16.51	7.8	7.8	6.2	6.2	--------	--------
1937														
Jan. 5	12:35 p. m.	43	LE	.4	6.6	7.0	4.85	8.77	7.3	7.4	Tr.	Tr.	--------	--------
27	11:45 a. m.	45	LF	.3	8.9	9.4	2.54	4.24	7.2	7.2	93.0	93.0	74.8	70.6
Feb. 11	12:10 p. m.	46	HWS	.4	5.6	4.1	11.17	12.12	7.6	7.6	Tr.	Tr.	--------	--------
Mar. 3	11:40 a. m.	47	LWS	.4	5.3	4.6	3.26	4.78	7.2	7.3	6.2	3.1	78.3	75.2
30	1:00 p. m.	49	LF	.4	8.5	8.3	10.86	10.73	8.3	8.4	Tr.	Tr.	96.9	95.3
Apr. 27	1:35 p. m.	50	LF	.4	15.1	14.3	7.47	8.73	--------	7.4	6.2	6.2	84.5	77.9
June 16	10:50 a. m.	51	LE	--------	23.4	23.4	6.40	9.06	--------	--------	12.4	12.4	--------	--------

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, LF=Last of flood, FF=First of flood, etc.
[2] Tr.=Trace.

TABLE 17.—*Hydrographic data for station 18 in the Pamunkey River above bridge at West Point*

[Average depth 29.5 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature		Salinity		pH		Phosphorus		Percentage saturation with dissolved oxygen	
					Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
				Meters	*° C.*	*° C.*	*Parts per thousand*	*Parts per thousand*			*Milligrams per cubic meter*	*Milligrams per cubic meter*		
1935														
Dec. 3	1:35 p. m.	4	FF	0.2	8.4	8.4	1.17	6.26	7.3	7.3	--------	--------	--------	--------
13	10:25 a. m.	5	FF	.6	6.4	6.3	7.12	9.07	7.6	7.6	--------	--------	80.9	80.8
1936														
Jan. 6	2:35 p. m.	7	LE	.2	1.3	1.3	.53	1.28	7.1	7.1	--------	--------	76.0	77.1
22	3:15 p. m.	8	LE	.2	3.4	3.2	.26	2.09	6.9	7.1	--------	--------	--------	--------
Feb. 20	3:15 p. m.	9	LE	.2	.2	.2	.14	.11	6.7	6.7	--------	--------	87.1	87.1
Mar. 6	10:05 a. m.	12	LF	.2	5.4	5.3	1.31	1.67	7.0	7.0	[2] Tr.	Tr.	--------	--------
19	1:15 p. m.	14	LWS	--------	10.7	10.5	.25	.17	7.1	7.2	6.0	--------	55.1	52.7
25	12:45 p. m.	16	HWS	.2	11.8	11.7	.25	.23	6.9	6.9	Tr.	Tr.	--------	--------
Apr. 1	12:30 p. m.	17	½E	.0	13.6	13.5	.23	.21	7.0	7.0	Tr.	Tr.	77.6	71.3
9	12:55 p. m.	18	LF	.2	12.2	12.2	.05	.12	7.1	7.0	43.4	6.2	--------	--------
16	2:30 p. m.	20	FF	.2	13.5	13.5	.05	.12	7.1	7.0	12.4	12.4	87.1	99.2
29	4:45 p. m.	21	FF	.1	15.8	15.5	.28	.28	7.0	7.0	8.0	--------	80.3	77.0
May 14	12:25 p. m.	22	½E	.3	21.9	21.8	.52	.61	7.2	7.1	Tr.	--------	--------	--------
June 3	12:50 p. m.	23	FF	--------	24.7	22.9	6.04	8.28	--------	--------	Tr.	2.0	101.6	86.6
July 2	10:45 a. m.	29	FE	.5	25.5	25.3	10.12	11.12	7.1	7.2	6.2	6.2	78.3	72.3
17	12:40 p. m.	31	FE	.5	29.3	28.3	11.08	12.94	7.0	7.1	3.1	3.1	--------	--------
31	2:30 p. m.	32	LE	.6	27.1	26.9	9.69	10.61	7.1	7.1	6.2	6.2	89.4	78.4
Aug. 17	12:20 p. m.	33	LF	.2	27.6	27.2	11.35	12.27	7.7	7.7	30.0	30.0	78.3	64.2
28	2:15 p. m.	34	FF	.7	28.3	28.4	11.58	11.43	7.4	7.1	12.4	12.4	95.6	83.3
Sept. 11	2:20 p. m.	35	LF	.6	26.2	25.6	11.44	12.57	7.2	7.2	3.1	3.1	84.6	69.0
Oct. 22	12:20 p. m.	37	FF	.8	20.2	19.7	9.58	10.03	7.8	7.8	12.4	12.4	76.4	68.6
Nov. 4	10:15 a. m.	38	LWS	.5	15.8	15.7	10.28	10.73	7.1	7.2	3.1	3.1	75.1	74.9
19	3:10 p. m.	39	LF	.5	9.3	9.1	14.25	14.38	7.6	7.5	--------	--------	--------	--------
Dec. 4	12:15 p. m.	40	LWS	.6	5.8	5.7	10.63	11.56	7.5	7.5	6.2	Tr.	--------	--------
5	2:30 p. m.	42	FE	.6	5.0	4.7	12.29	14.20	7.7	7.7	6.2	12.4	--------	--------
1937														
Jan. 5	2:45 p. m.	43	FF	.1	6.3	6.5	.60	3.32	7.2	7.3	68.2	Tr.	--------	--------
27	1:00 p. m.	45	HWS	.1	8.5	8.5	.21	.58	6.9	7.0	12.4	12.4	57.7	54.7
Feb. 11	10:40 a. m.	46	LF	.2	5.8	5.0	4.45	6.83	7.3	7.3	Tr.	Tr.	--------	--------
Mar. 3	1:20 p. m.	47	FF	.2	5.0	5.0	.15	.24	7.1	7.1	8.0	8.0	68.3	77.0
30	2:50 p. m.	49	HWS	.4	9.3	8.3	7.34	8.77	8.2	8.2	Tr.	Tr.	95.0	89.4
Apr. 27	2:30 p. m.	50	HWS	.3	15.7	15.0	3.19	4.89	7.2	--------	Tr.	Tr.	71.1	75.0
May 17	3:00 p. m.	50a	LF	--------	19.7	19.9	.12	.12	6.7	6.8	--------	--------	65.8	65.3

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, LF=Last of flood, FF=First of flood, etc.
[2] Tr.=Trace.

TABLE 18.—*Hydrographic data for station 19 in the Mattaponi River above the bridge at West Point*

[Average depth 15.0 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature		Salinity		pH		Phosphorus		Percentage saturation with dissolved oxygen	
					Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
				Meters	*° C.*	*° C.*	*Parts per thousand*	*Parts per thousand*			*Milligrams per cubic meter*	*Milligrams per cubic meter*		
1935														
Dec. 3	2:50 p. m.	4	FF	0.6	8.3	8.1	3.91	4.78	7.3	7.3	----	----	----	----
13	9:25 a. m.	5	FF	.7	6.3	6.2	4.29	6.96	7.3	7.6	----	----	82.3	82.9
1936														
Jan. 6	3:35 p. m.	7	LE	.2	1.2	1.1	.07	.07	7.2	6.7	----	----	82.3	71.3
Mar. 6	11:10 a. m.	12	FE	.2	5.7	5.3	1.69	1.98	7.0	7.0	[2] Tr.	Tr.	----	----
19	12:30 p. m.	14	LE	----	10.8	10.5	.04	.04	7.1	7.2	----	----	86.1	85.7
25	12:00 m.	16	LF	.1	11.7	11.6	.10	.08	6.7	6.7	8.0	Tr.	----	----
Apr. 1	11:35 a. m.	17	½E	.2	13.8	13.7	.10	.10	7.0	6.9	Tr.	Tr.	91.7	78.8
9	11:50 a. m.	18	LF	.2	12.2	12.2	----	----	6.9	6.9	92.4	12.2	----	----
16	1:30 p. m.	20	LWS	.4	13.1	13.0	.07	.07	6.9	6.9	15.0	12.4	94.0	103.5
29	2:40 p. m.	21	FF	.2	16.3	15.5	.10	.10	6.8	6.7	12.4	12.4	90.0	82.9
June 3	12:30 p. m.	23	HWS	.6	24.1	22.8	6.46	6.73	----	----	Tr.	Tr.	81.1	87.9
July 2	10:00 a. m.	29	FE	.6	25.5	25.4	9.49	10.14	7.1	7.3	6.2	6.2	83.8	76.8
17	11:25 a. m.	31	FE	.6	28.7	27.9	12.14	12.52	7.1	7.3	3.1	3.1	----	----
31	3:30 p. m.	32	LE	.6	27.1	26.7	7.23	9.86	----	----	12.4	0	86.7	64.4
Aug. 17	11:15 a. m.	33	LF	.5	27.2	27.2	10.75	11.35	7.8	7.7	30.0	30.0	93.5	69.7
28	3:00 p. m.	34	FF	.8	28.5	28.1	11.76	11.91	7.2	7.2	12.4	12.4	76.8	77.0
Sept. 11	1:05 p. m.	35	LE	.5	26.2	25.9	11.33	11.82	7.0	7.2	3.1	3.1	86.5	83.8
Oct. 22	1:40 p. m.	37	FF	.7	19.9	19.7	12.25	12.32	7.9	7.8	12.4	12.4	79.3	78.4
Nov. 4	9:30 a. m.	38	LWS	.6	15.7	15.5	9.81	10.55	7.2	7.1	3.1	3.1	84.4	83.4
19	2:45 p. m.	39	LF	.7	9.2	9.2	13.44	14.02	7.6	7.6	----	----	----	----
Dec. 4	11:25 a. m.	40	LWS	.7	5.7	5.5	10.48	11.91	7.6	7.6	6.2	6.2	----	----
15	3:15 p. m.	42	FE	1.1	5.2	4.9	11.98	12.86	7.7	7.6	6.2	6.2	----	----
1937														
Jan. 5	2:00 p. m.	43	FF	.3	6.4	6.3	.96	1.56	7.1	7.1	74.4	12.4	----	----
27	12:15 p. m.	45	HWS	.2	8.9	8.9	.19	.40	6.9	6.8	12.4	12.4	62.8	68.8
Feb. 11	10:00 a. m.	46	LF	.2	4.9	4.5	3.57	4.87	7.2	7.3	Tr.	Tr.	----	----
Mar. 3	12:30 p. m.	47	LWS	.2	5.2	5.0	.12	.12	6.9	6.8	8.0	8.0	69.1	53.4
30	2:15 p. m.	49	HWS	.4	9.1	8.7	6.17	7.29	8.2	8.2	Tr.	Tr.	91.5	89.6
Apr. 27	3:00 p. m.	50	FE	.3	16.1	15.9	2.67	3.73	----	----	Tr.	Tr.	75.5	70.6

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, LF=Last of flood, FF=First of flood, etc.
[2] Tr.=Trace.

TABLE 19.—*Hydrographic data for station 55 in the lower Piankatank River off Iron Point*

[Average depth 4.2 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature	Salinity	pH	Phosphorus	Percentage saturation with dissolved oxygen
				Meters	*° C.*	*Parts per thousand*		*Milligrams per cubic meter*	
1935									
Dec. 10	1:50 p. m.	2	½E	[2] B	6.6	17.56	8.1	----	101.4
1936									
Jan. 11	12:25 p. m.	3	FF	B	2.2	13.75	7.9	----	97.0
Mar. 3	1:30 p. m.	4	FF	B	4.3	11.17	8.1	----	108.6
12	2:00 p. m.	5	FE	----	7.0	11.73	7.9	[3] Tr.	73.1
Apr. 3	10:15 a. m.	6	LE	B	11.9	10.14	8.3	Tr.	102.9
16	10:30 a. m.	7	LE	B	13.2	8.42	8.4	Tr.	106.7
May 6	9:25 a. m.	8	LF	B	18.8	8.06	8.3	Tr.	103.3
June 4	11:00 a. m.	9	FE	B	23.2	10.86	----	92.0	90.3
16	10:00 a. m.	10	FE	B	24.5	11.73	7.7	3.0	----
July 1	10:00 a. m.	11	½E	B	25.0	12.67	8.1	3.0	91.9
21	10:40 a. m.	12	FE	B	27.2	14.22	7.4	6.2	----
Aug. 3	10:30 a. m.	13	½F	B	25.7	16.04	7.8	8.0	87.7
21	10:15 a. m.	14	LF	----	28.0	16.46	7.9	12.4	106.5
Sept. 3	9:15 a. m.	15	HWS	----	25.2	18.01	7.7	6.2	96.0
Oct. 6	10:30 a. m.	17	HWS	B	21.0	18.57	7.9	3.1	97.6
26	11:45 a. m.	18	½F	B	19.0	19.05	7.9	3.1	96.4
Nov. 10	10:30 a. m.	19	FE	B	13.7	19.40	8.0	----	112.2
Dec. 1	10:15 a. m.	21	HWS	B	5.3	19.67	8.0	3.1	----
1937									
Jan. 12	10:30 a. m.	22	FE	B	8.1	17.32	8.1	Tr.	----
Feb. 2	10:10 a. m.	24	LE	B	6.7	13.64	7.6	Tr.	99.2
16	9:45 a. m.	25	½F	----	5.4	12.43	7.8	----	99.2
Mar. 2	10:30 a. m.	26	LE	B	3.9	12.57	7.9	24.8	----
23	9:30 a. m.	27	FE	B	8.1	11.35	----	3.1	----
Apr. 6	10:15 a. m.	28	FE	B	10.7	13.15	8.6	5.0	113.6
21	9:45 a. m.	29	HWS	B	15.1	13.37	8.6	----	111.4

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, FE=First of ebb, FF=First of flood, etc.
[2] B=On the bottom.
[3] Tr.=Trace.

TABLE 20.—*Hydrographic data for station 53 in the upper Piankatank River off Ferry Creek*

[Average depth 7.3 feet]

Date	Time	Cruise	Tide [1]	Turbidity disc reading	Water temperature		Salinity		pH		Phosphorus		Percentage saturation with dissolved oxygen	
					Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
				Meters	*° C.*	*° C.*	*Parts per thousand*	*Parts per thousand*			*Milligrams per cubic meter*	*Milligrams per cubic meter*		
1935														
Nov. 13	2:40 p. m.	1	½E	----	17.4	16.8	13.33	14.51	----	----	----	----	----	----
Dec. 10	11:30 a. m.	2	HWS	2.2	7.1	7.1	13.33	13.73	8.0	8.0	----	----	97.4	100.7
1936														
Jan. 11	11:20 a. m.	3	FF	1.8	3.0	2.5	7.48	12.00	7.8	7.8	----	----	91.2	92.4
Mar. 3	11:40 a. m.	4	FE	2.2	----	5.1	----	6.11	----	7.5	----	----	----	99.4
12	12:45 p. m.	5	HWS	1.3	9.2	9.1	7.21	7.27	7.6	7.6	[2] Tr.	Tr.	75.8	75.7
Apr. 3	12:10 p. m.	6	LE	1.3	----	12.9	----	7.18	----	7.9	----	Tr.	----	97.8
16	11:45 a. m.	7	LE	----	----	14.9	----	5.63	----	8.1	----	Tr.	----	98.4
May 6	11:00 a. m.	8	LF	1.2	20.2	19.7	5.54	6.00	8.0	8.0	Tr.	Tr.	91.4	93.9
June 4	12:30 p. m.	9	½E	1.2	24.3	24.4	9.60	9.43	----	----	6.2	3.0	96.1	76.0
16	11:00 a. m.	10	FE	----	----	25.3	----	9.65	----	7.5	----	6.2	----	----
July 1	11:30 a. m.	11	LE	----	----	25.8	----	10.75	----	7.6	----	Tr.	----	77.9
21	12:40 p. m.	12	FE	.8	27.7	27.9	12.48	12.70	7.2	7.2	6.2	6.2	----	----
Aug. 3	12:00 m.	13	LF	.5	27.3	26.3	14.16	14.67	7.5	7.5	4.0	6.2	79.8	82.6
21	11:20 a. m.	14	LF	----	28.6	27.5	13.26	15.25	7.9	7.7	12.4	12.4	110.3	66.8
Sept. 3	11:45 a. m.	15	LE	----	26.0	25.4	16.04	16.26	7.7	7.8	6.2	6.2	100.4	101.6
Oct. 6	12:00 m.	17	FF	1.0	20.8	21.3	16.80	17.09	7.9	7.8	3.6	6.2	105.8	97.4
26	1:00 p. m.	18	LF	----	18.9	18.9	17.45	17.34	7.9	7.8	3.1	3.1	92.6	94.0
Nov. 10	11:45 a. m.	19	FF	2.0	14.1	14.1	17.90	17.88	7.9	7.9	----	----	98.1	100.8
Dec. 1	12:30 p. m.	21	FE	1.6	4.2	4.3	17.57	17.57	8.0	7.9	3.1	3.1	----	----
1937														
Jan. 12	2:30 p. m.	22	LWS	1.7	8.9	8.9	12.25	12.47	7.9	7.9	Tr.	Tr.	----	----
Feb. 2	11:50 a. m.	24	LE	.7	6.2	6.1	7.14	7.05	7.5	7.1	Tr.	Tr.	86.7	78.0
16	11:00 a. m.	25	½F	1.7	5.9	5.7	8.33	8.28	7.5	7.7	----	----	106.2	101.8
Mar. 2	12:00 m.	26	FF	1.8	----	3.8	----	7.85	----	----	----	24.8	----	----
23	10:45 a. m.	27	FE	2.0	8.9	8.8	9.16	10.23	----	----	3.1	6.2	----	----
Apr. 6	12:00 m.	28	½E	1.0	13.1	12.7	9.02	9.07	8.4	8.4	5.0	5.0	105.3	105.0
21	10:45 a. m.	29	FE	1.4	16.1	14.1	10.35	13.46	8.6	8.6	----	----	117.7	113.5

[1] LWS=Low water slack, HWS=High water slack, LE=Last of ebb, LF=Last of flood, FF=First of flood, etc.
[2] Tr.=Trace.

UNITED STATES DEPARTMENT OF THE INTERIOR, J. A. KRUG, *Secretary*
FISH AND WILDLIFE SERVICE, ALBERT M. DAY, *Director*

CONTRIBUTIONS TO THE BIOLOGY OF THE PACIFIC TUNAS

BY MILNER B. SCHAEFER AND JOHN C. MARR
AQUATIC BIOLOGISTS

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SPAWNING OF YELLOWFIN TUNA (*NEOTHUNNUS MACROPTERUS*) AND SKIPJACK (*KATSUWONUS PELAMIS*) IN THE PACIFIC OCEAN OFF CENTRAL AMERICA, WITH DESCRIPTIONS OF JUVENILES

By Milner B. Schaefer and John C. Marr

Although the commercial fishery for Pacific tunas has become one of the leading fisheries of the United States, being in value second only to salmon, the life histories of the species which furnish the raw material of this industry are little known. An opportunity to conduct preliminary studies of the biology of these important fishes became available during the late winter and spring of 1947 when the factory ship *Pacific Explorer*, operated by the Pacific Exploration Co., made a voyage to Costa Rica for a cargo of frozen tuna. The authors, who were aboard this vessel and the fishing craft supplying her, as scientific observers of the Fish and Wildlife Service, were able to gather material in waters off Costa Rica between January 21 and May 10, 1947.

It was particularly fortunate that this trip occurred at a season when it was possible to obtain valuable data on the reproduction of the tunas. The places and seasons of spawning of Pacific tunas have long been a mystery. The only reference we have found in the literature to the location of a tuna spawning area in the Pacific is a Japanese paper, cited by Fisher (1947), by an unknown author (Anon. 1942) the title of which indicates that at least one species spawns in the vicinity of the Palau Islands. We have not yet been able to examine a copy of this paper. Kishinouye (1923) made a few incidental remarks on the occurrence of maturing and spent specimens of *Thunnus orientalis* (Temminck and Schlegel) in the summer fishery along the Japanese coast, and on the spawning of *Euthynnus yaito* Kishinouye, which "seems to take place about May in Taiwan." Of *Auxis hira* Kishinouye, he said, "seem to spawn in summer. Reproductive elements are ripe in August."

OBSERVATIONS ON ADULTS

Neothunnus macropterus (Temminck and Schlegel 1850)

The yellowfin tuna was the principal species caught during this voyage of the *Pacific Explorer*. Some 2,200 tons of this species were taken, compared with about a tenth of this amount of skipjack.

In the first catches examined, in late January, most of the larger fish, those more than about a meter in length, were in rather advanced stages of sexual maturity as judged by examination of the gonads. This condition was typical of these large yellowfin through February. The upper panel of figure 1 shows the size composition of representative samples of the catch during late January and early February. Smaller fish, below about a meter in total length, were in many cases found to have gonads little developed at this time. Many of the maturing fish examined seemed to be imminently ready to spawn, although no running-ripe specimens were captured. Females were taken in which the ovaries were large and turgid and filled with relatively large, yolk-filled ova measuring about 0.6 mm. in diameter (measured as formalin-preserved material). Several males were taken with running milt in the central duct of the testis.

Ova of the above diameter have probably attained nearly full size, as judged by information available on other species. Ova from a preserved ovary of a running-ripe *Euthynnus lineatus* Kishinouye from Costa Rica measure 0.72 mm. to 0.81 mm. in diameter. Sanzo (1929) stated that the fertilized ovum of *Thunnus thynnus* (Linnaeus) of the Mediterranean is between 1.0 mm. and 1.12 mm. This is larger than the ova in the ovary because the diameter is increased by absorption of water after the ovum is liberated into the sea.

As the season progressed, the largest yellowfin (fig. 1), became relatively less numerous in the landings. At the same time, examination of the gonads showed that the smaller fish were on the average in more advanced stages of maturity than those examined earlier. In April many of the fish down to 70 cm. in length appeared almost ready to spawn.

It may be seen from figure 1 that there was also a group of small fish, of a modal length of about 60 cm., which were particularly numerous in the purse-

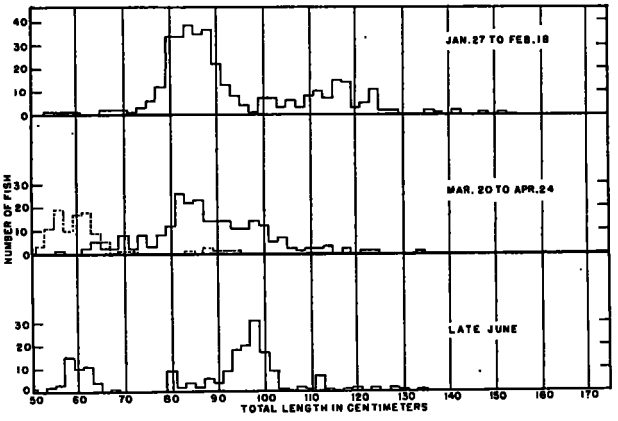

FIGURE 1.—Length frequencies of samples of catches of *Neothunnus macropterus* off Costa Rica. Solid lines represent catches by bait boats. Broken lines show catches by purse seiners.

seine catches in March and April. The gonads of these fish were completely immature in all samples taken, and it is presumed that these fish represent an age group which has not attained the age of first spawning.

It must be noted that our studies of the gonads are based on relatively few samples. Since it is the commercial practice to freeze tuna in the round, we were not able to open large numbers of specimens, because this decreases their commercial value. We examined about 150 specimens from 15 landings. To make any quantitative study of the relative degrees of maturity of different size groups would, of course, necessitate much more extensive sampling.

Our observations were discontinued in Costa Rica in early May, and the ship returned to her home port early in July. Two large bait-boat catches of yellowfin tuna made off Costa Rica during the last week in June had been taken aboard the mother ship just before her departure and were stowed so that they were separable from the remainder of the cargo. These fish were processed at the cannery immediately after unloading and were examined at that time for sexual condition. The size composition of these landings is shown in the lower panel of figure 1. The fish of the small size group, near 60 cm., were all completely immature, as were those examined before. The larger fish, of which more than 50 were examined, were all spent, some apparently rather recently so.

These observations indicate that the yellowfin tuna spawn somewhere in the vicinity of Costa Rica in the early spring months. The capture of fish in advanced stages of maturity during a 3-month period indicates that the spawning season is rather long. It seems also that the smaller tuna tend to mature somewhat later than the larger ones. This conclusion corresponds to the results obtained for *T. thynnus* of the Mediterranean. Heldt (1930) stated—

> Sella fait remarquer qu'il y a lieu de distinguer ici suivant la taille des sujets. Les petits thons marquent effectivement un retard dans leur formation, ce qui fait que pour eux la ponte est plus tardive. Sur les côtes de Sicile, par example, la ponte commence dès juin et se termine dans la second décade de juillet pour les thons gros et moyens; elle se prolonge jusqu'en août pour les petits. Il arrive même de trouver en Adriatique, en août, de petits thons avec des boutargues développées.

T. thynnus is captured in the Atlantic, along the southern coasts of Spain and Portugal, and along the shores of the Mediterranean by means of pound nets, or "madragues." Tunas in various stages of maturation are taken during the direct migration, the "époque du course," and spent fish are taken later during the "époque de retour." Running-ripe males are sometimes captured, but fully ripe females are seldom taken. (Heldt 1930; Frade and Manaças 1933; Frade 1937). According to Heldt (1930), Sella thinks—

> Pour l'émission des produits sexuels l'animal accomplirait un mouvement au large, probablement assez limité. Il est possible * * * que ce mouvement ne se produise pas une seule fois, mais qu'il y ait une succession d'éloignments et de rapprochements de la côte, ce qui expliquerait la présence dans les boutargues de fin de saison du course de glandes partiellment vidées.

He also gives deBuen as the authority that "Les différentes phases de dévelopment et les diamètres variés des ovules qui s'y trouvent prouvent en effet que la ponte doit être fractionnée." Frade and Manaças (1933), by a histological study of the gonads, demonstrated that all the ova are not matured at once but that they are developed and spawned fractionally.

It seems likely that a similar spawning of several batches of ova occurs in *N. macropterus*. Measurement of the sizes of ova in an ovary in an advanced stage showed that in addition to the largest group of ova, near 0.65 mm., there is another pronounced mode near 0.44 mm. representing, presumably, the group maturing for the next spawning.

Our failure to observe any running-ripe females and the disappearance of the largest fish from the bait-boat catches as the season progressed might be taken to indicate that as the fish mature they migrate elsewhere for spawning. If so, it must be to

a place in the vicinity, since, as will be shown later, juvenile tunas as small as one centimeter were captured off Costa Rica, and it seems unlikely that these had migrated very far. An alternative hypothesis is that as the tunas approach spawning time they cease feeding, and so are not taken by fishermen on the bait boats. Even fish in less advanced stages of maturity probably do not feed as actively as during the season of sexual inactivity. Many schools encountered on this voyage were notably disinclined to take live bait, and time after time not a single fish was captured from a large school. The catch statistics and the experience of the fishermen reflect the poorness of the bait fishing in the late winter and spring months, and indicate that the yellowfin normally do not bite well during this season. Purse-seine catches examined (fig. 1) consisted almost entirely of fish of the size group which is completely immature.

Katsuwonus pelamis (Linnaeus 1758)

Very few skipjack were taken by bait boats during the period of our observations, but purse seine fishermen who operated in the area in late March and April were more successful. Six specimens were examined from a catch of a few hundred pounds made by a bait boat on February 21. These six specimens, four males and two females, were maturing, one male and one female appearing to be imminently ready to spawn. From a purse-seine catch on March 30, four females and six males were examined; the four females all appeared to be spent fish, having flaccid, empty gonads; the males were either spent or just beginning to mature, these two stages appearing much the same in male fishes.

OBSERVATIONS ON JUVENILES

When overtaken by darkness on the fishing grounds, the fishing vessels heave to and drift until daylight, unless it is desired to move to a new locality for the next day's fishing. When aboard such vessels at night, we took advantage of the opportunity to collect organisms attracted to a drop light suspended outboard close above the surface of the water. A large number of species of fishes and other organisms were collected in this manner, including juveniles of four species of scombroid fishes belonging to the genera *Neothunnus*, *Katsuwonus*, *Euthynnus*, and *Auxis* (Schaefer and Marr 1948). In this paper we shall deal only with the juveniles of the yellowfin tuna, *Neothunnus*, and the skipjack, *Katsuwonus*.

The positive phototropism of very young tunas in the Mediterranean has been noted by several authors. Sparta (1933) collected post-larval *T. thynnus* and *Auxis bisus* Bp. (=*A. thazard* Lacépède) by this means. Sella (1929) refers to the collection of young stages of *T. thynnus* under lights. According to Heldt (1928), Sanzo has found that young *T. thynnus* up to 15 cm. are attracted by light, but that above this size they develop a negative phototropism.

Neothunnus macropterus

Among the scombroid fishes collected by drop-light fishing is a series, which we regard as *N. macrop-terus*, characterized by a relatively deep body, and by heavy pigmentation of the first dorsal fin, the posterior edge of which reaches almost to the insertion of the second dorsal. Photographs of representative specimens of the series, preserved in alcohol, are shown in figure 2, and a 19-mm. specimen is drawn in figure 3. Specimens of this sort were collected at the following localities on the dates indicated: 2 specimens, 14 and 15 mm. total length, from 9°22.5′ N., 85°47.5′ W., Jan. 28, 1947. (These and other total-length measurements in this paper were taken from the tip of the snout to the tip of the shortest median ray of the caudal fin.) Six specimens, 26 mm. to 43 mm. total length, from 9°10′ N., 85°20′ W. March 20, 1947; 20 specimens, 10 mm. to 24 mm. total length, from 9°20′ N., 85°10′ W. April 1, 1947; 1 specimen, 41 mm. total length, from 8°7.5′ N., 83°8.5′ W., May 7, 1947.

In addition to the examination of specimens in alcohol, 4 specimens of 15, 18, 31, and 43 mm. were prepared for study of the bony parts by staining in alizarin and clearing, according to the procedure of Hollister (1934).

As illustrated in figure 2, fish of all sizes had a heavily pigmented first dorsal fin. The second dorsal fin remains unpigmented until the fish reaches about 24 mm., when the lower part of the second dorsal fin begins to assume a dark coloration. In specimens from about 30 mm. up to the largest in our collections, the second dorsal fin is pigmented rather heavily in its lower half; the distal half remains unpigmented. In addition to that of the first dorsal fin, there is no external dark pigmentation of the smallest individuals, 10 mm. to 12 mm., except a thin strip on the back at the base of the first dorsal fin. There is a dark area on the top of the head forward of the nape, which is subcutaneous, being the pigmented covering of the brain. At 16 mm. the tips of the jaws are lightly pigmented, as are the sides of the

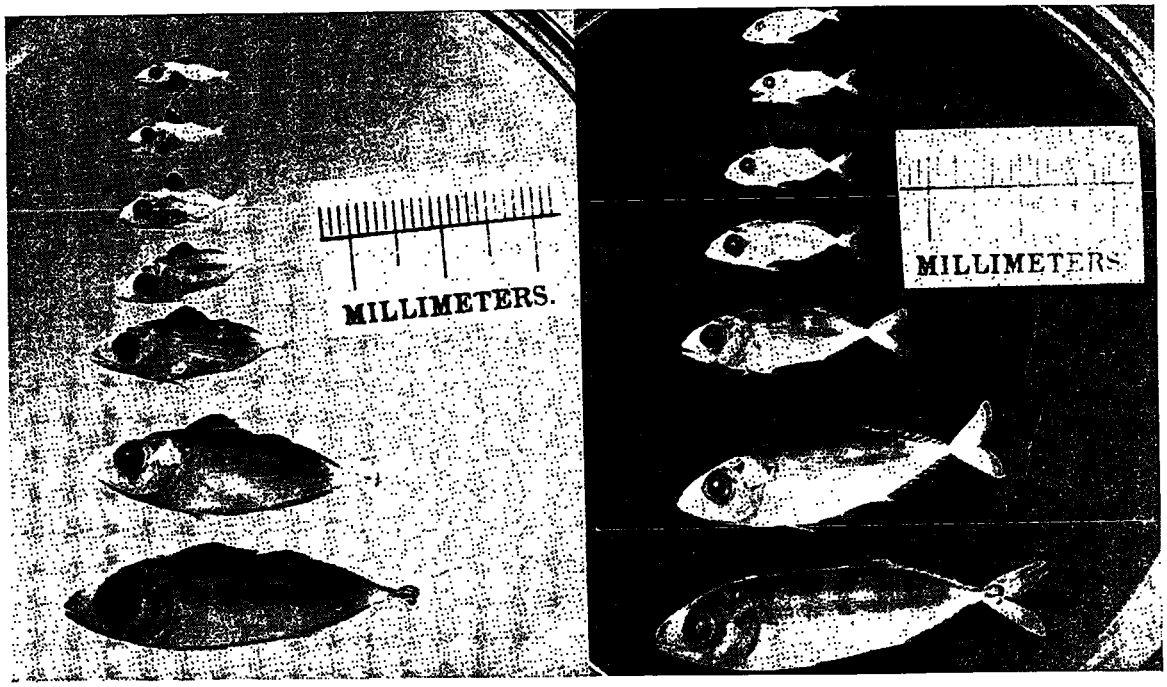

FIGURE 2.—Juvenile *Neothunnus macropterus* photographed against light and dark backgrounds.

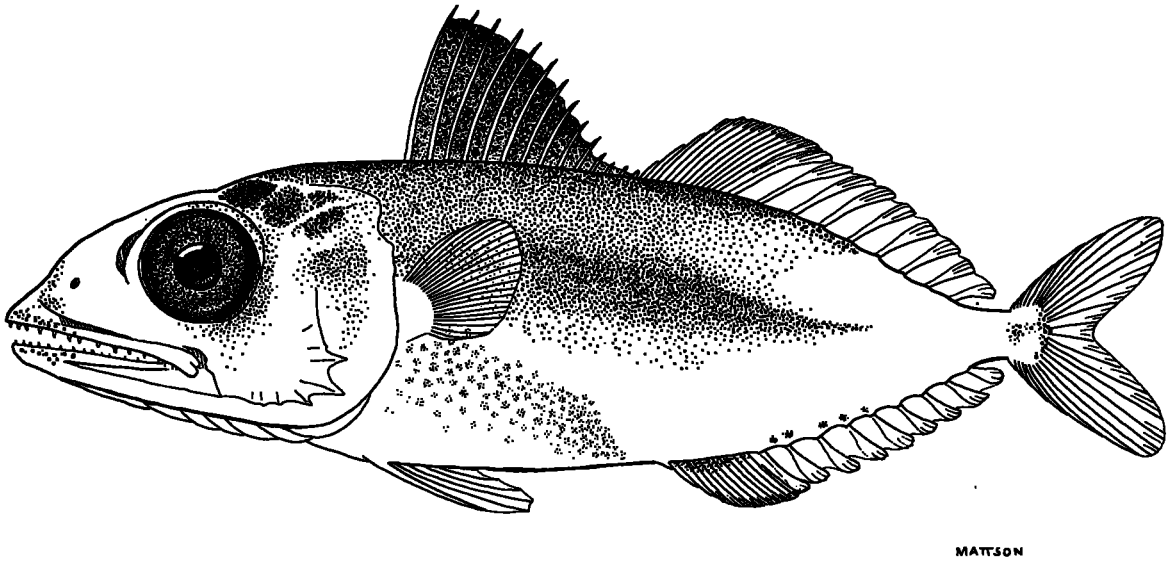

FIGURE 3.—*Neothunnus macropterus*, 19 millimeters long.

body down to the midline and posteriorly to about the level of the posterior edge of the second dorsal fin. The pigmentation of the body deepens, and extends farther down the sides and farther back at 19 mm., the operculum becomes lightly pigmented, while the posterior margin of the orbit is rather heavily darkened, and the posterior dorsal region of the head bears large pigmented areas. On a 24-mm. specimen there is, in addition, a little dark pigment on the bases of the caudal rays, and the dark pigment on the back and upper sides begins to become concentrated in patches which in larger specimens form five dark vertical bars. The peritoneum of juveniles of all sizes in our collections bears numerous closely spaced black spots. In fishes below about 25 mm. these may be seen through the body wall.

On the smallest specimens there are three prominent spines at the lower posterior angle of the preoperculum, with two lesser spines on the vertical margin above, and two on the horizontal margin forward of the larger spines. These spines become less and less prominent as the bone of the preoperculum grows to fill in the spaces between them until they are not easily discernible in a specimen of 24 mm. and are quite absent in a specimen of 35 mm.

Examination of the vertebral columns of the four alizarin-stained specimens showed the vertebrae to be 18 precaudal and 21 caudal in each case (counting the urostyle), bearing closed haemal arches on some precaudal as well as on the caudal vertebrae. In the largest specimen the muscles were dissected away from one side to allow a careful examination from which it was possible to determine with certainty that the first closed haemal arch occurs on the eleventh vertebra. The 15-mm. and 18-mm. specimens were determined with some uncertainty to have the first closed haemal arch on the tenth and eleventh vertebrae, respectively. Determination was not possible on the 31-mm. specimen without dissection, and this was not desirable. On all specimens the haemal canal is large; beneath the posterior precaudal and anterior caudal vertebrae it is as wide as or wider than the vertebral column. Inferior foramina are not yet developed on any of the vertebrae of the 15-mm. or 18-mm. specimens, but in the 31-mm. and 43-mm. specimens there are moderately large, well-developed inferior foramina on the fourth to fourteenth caudal vertebrae. These foramina become progressively smaller going posteriorly. There are no ventral foramina on any precaudal vertebrae. The characteristic lateral processes on the posterior caudal vertebrae (Kishinouye 1923; Frade 1932) are not yet developed in the two smallest specimens, but are slightly developed in the 31-mm. specimen and are quite well developed in the 43-mm. specimen. The lateral processes of the anterior precaudal vertebrae are not yet developed in any of our specimens.

The pectoral fin has 31 and 35 rays, respectively, on the two largest stained specimens. The first dorsal fin has 14 spines in all 4 specimens, but in one of these the last spine is completely subcutaneous and would not be observed except in a special preparation. The first spine is usually the longest one, but sometimes it is the second. The combined count of second dorsal rays and of dorsal finlets was found to be 23 in each of 3 specimens and 22 in 1. The finlets appear to be eight or nine in number, it being impossible to distinguish accurately between the last ray of the second dorsal fin and the first finlet. The combined count of anal rays and anal finlets is 22 in all 4 specimens. The anal finlets are eight or nine, it again being impossible to distinguish accurately which is the first finlet behind the fin.

In the smallest specimens the finlets are connected together and to the fin by a continuous membrane extending almost to the tips of the finlets. As the fish grows, this membrane gradually disappears except sometimes between the fin and the first, or the first and second, finlets behind the fin. In specimens of 25 mm. the membrane extends only about half way to the tips of the finlets. At 40 mm. it has almost completely disappeared, there being only a remnant at the bases of the finlets.

The intestine passes posteriorly along the right side of the body cavity. It is straight, without a fold, in specimens below about 35 mm., at which size there is a slight kink which is the beginning of the formation of the folds. In fishes of 40-mm. total length the intestine has the two folds characteristic of adult Thunnidae, but the ascending portion of the intestine between folds is relatively much shorter than in adults.

The liver was examined in six specimens from 24 mm. to 43 mm. in total length. In each case the right lobe was noticeably larger than the center or left lobes, which were nearly equal in size. In one case the left lobe was itself divided into two parts.

The anterior portion of the lateral line is visible in specimens of more than about 24 mm. in length. Its unusual course above the pectoral fin is that peculiar to the Thunnidae (Kishinouye 1923; p. 304 and pl. XXVI and XXVII).

The gill rakers on the first arch are just becoming visible as very small projections in fishes 18 mm. long, and cannot be counted with any accuracy. At 31 mm. the gill rakers are still very short and were counted as 6+18. At 40 mm. they are fairly well developed and can be counted with better accuracy; those of a 41-mm. specimen were counted as 8+21 and of a 43 mm. specimen as 7+20.

The specimens of this series are readily identified as belonging to Kishinouye's family Thunnidae by the vertebrae (18+21 in number, with complete haemal arches on some, but no inferior foramina on any, of the precaudal vertebrae), by the shape of the lateral line, and by the folded intestine. Of the four species of this family which are known from the eastern Pacific, two, *T. thynnus* and *Thunnus germo*

(Lacépède), have ranges which probably do not extend to the latitudes of Central America. Herre (1936) has recorded *T. thynnus* from the Galapagos Islands, but this seems likely to be in error. In any event, our specimens may be shown as not belonging to these species because in the genus *Thunnus* the first complete haemal arch occurs typically on the tenth vertebra (Godsil and Byers 1944; Frade 1932), the inferior foramina on the vertebrae are very poorly developed (Kishinouye 1923), and the center lobe of the liver is the largest of the three (Kishinouye 1923; Godsil and Byers 1944).

There remains then to decide to which of the remaining two species, *Parathunnus mebachi* (Kishinouye) or *Neothunnus macropterus*, both of which occur in the region of this study, our specimens belong. (*P. mebachi* is seldom taken in the commercial catches.) Many of the characters pointed out by Godsil and Byers (1944) are not available for our purpose. The relative lengths of the intestinal folds cannot be used because this is changing rapidly in these juvenile fishes. The same is true of the size and shape of the air bladder. The shape of the postero-ventral margin of the cranium, which these authors stated to be "the most useful and distinctive difference," resembles that of the adult *Neothunnus*, but again this character is probably undergoing modification and is, therefore, not reliable. The peculiarities in the circulatory system, which is the basis of Kishinouye's differentiation of *Parathunnus*, cannot be studied in our small specimens.

We have concluded that these specimens are most probably *N. macropterus* for the following reasons: The haemal canal is large, being as broad as the vertebral column beneath the posterior precaudal and anterior caudal vertebrae, and the inferior foramina on the caudal vertebrae are well developed. Both of these characters correspond to those of adult *Neothunnus* and differ from those of adult *Parathunnus* in which the haemal canal is narrow and in which the inferior foramina are poorly developed. If the assumption is correct that these characteristics are fixed at these early stages, this is definitive. The larger right lobe of the liver is also definitive according to Kishinouye (1923, p. 363), but Godsil and Byers state that in one of their two specimens of *Parathunnus* the right lobe was "slightly the longest." It seems most probable, therefore, that our juveniles are *N. macropterus*, but there is some possibility they may be *P. mebachi*. This problem cannot be settled with certainty until juveniles of both species are available for comparison.

Lütken (1880) depicted in his plate III, figures 1 and 2, juvenile tunas 17 mm. and 10 mm. in length which may perhaps be juvenile *Neothunnus*. He identified them as being probably juveniles of *Orcynus germo* (Lac.), in which species he includes all the "long-winged" tunas. He wrote:

> These tuna fishes with the long pectoral fins which the seamen generally call "Albacora" or "Albicora" are divided into a whole series of species: *Th. alalonga*, *albacora*, *germo*, *pacificus*, *argentivittatus*, *balteatus*, *sibi* and *macropterus*, all of which, perhaps, represent only one species which most fittingly could be called *Orcynus germo* (Lac.)

Thus, he included in this single species the yellowfin tunas, *Neothunnus*, the Atlantic and Pacific forms of which, at least, now appear to be distinct (Frade 1931), and the albacore or germon *T. germo*.

Lütken's figures of these juveniles show the posterior quarter of the first dorsal as being unpigmented, or lightly pigmented, while the anterior three-quarters appears heavily pigmented. This is not mentioned in the text. Otherwise the figures are very similar to our specimens. His 17-mm. specimen was taken by the *Galatheas* on June 3, 1836 in a tow net at an unspecified location (probably in the East Indies since the ship was at Singapore on August 9). Lütken described this specimen:

> * * * rather plump and short; the height one quarter of the total length, and the length of the head contained 2½ times in the latter. Sparse teeth, palatine teeth; 5 to 6 spines on the anterior gill cover. The finlets could hardly be said to be present as they were too closely situated, but 8 or 9 rays could be identified. The sides of the head behind the large eyes, which took up almost the whole height of the head, and the sides of the abdomen were of shiny silvery color; otherwise, the fish was dark.

Of smaller specimens, taken at a number of localities in the Atlantic Ocean and at one station in the South China Sea on unspecified dates, he said:

> The author strongly suspects that some even smaller fishes (8 to 10 mm.) represent developmental stages of the same type. These small fishes are completely colorless except for the eyes and first dorsal fin, which are black. They are noticeably short with large heads, the latter being almost as long as the rest of the body. Three anterior gill cover spines are visible. The mouth slit reaches till under the middle of the eye. At the most 14 scattered curved teeth in each mandibular row. No trace of "pinnulae"; however, in the larger ones, one can point out the eight or nine rays which later will form such "pinnulae."

Ehrenbaum (1924) found among the *Thor* collections, made with the young-fish trawl in the Medi-

terranean and Atlantic, two kinds of tuna larvae which, following Lütken's terminology, he referred to the genus *Orcynus* (=*Thunnus*) on the basis of vertebral counts of 18+21 and other characters. These larvae, the largest of which was 13.5 mm. long, preserved, were too small to identify as to species by morphological characteristics. Ehrenbaum considers only two species of the genus to occur in these waters, the "red" tuna *O. thunnus* L. and the "white" tuna, or germon, *O. germo* (Lac.). He tentatively identified the larvae in question with these two species on the basis of their relative abundance:

In Ermangelung eines zuverlässigen Unterscheidungsmerkmals habe ich mich nun entschlossen, die in Mittelmeer häufigere Larvenform dem grossen Thun, die im Atlantik häufigere dem Germon zuzuteilen. Das kann mit Recht als unzulässig bezeichnet werden; aber ich tue es auf die Gefahr hin, eine spätere Korrektur zu erfahren; * * *

We have compared our smallest specimens of *N. macropterus* in detail with Ehrenbaum's descriptions of *O. germo* of similar size (pp. 20–22). They agree in all respects with the exception of the pigmentation of the first dorsal, and perhaps the preopercular spines. It should be noted that the nasal "rosette" is a subcutaneous structure visible in our material only in a carmine-stained and cleared specimen. His specimens have the first dorsal fin only partly pigmented whereas ours have it completely covered with heavy pigmentation at all sizes, including those corresponding in size to his larvae. The preopercular spines on his larvae of 12 mm. to 13.6 mm. as described and figured appear one or two more numerous than on our specimens of similar sizes. It seems likely that these specimens may be the young of *Neothunnus albacora* (Lowe), because of the similarity to our specimens of *N. macropterus*. They may, however, be young *T. germo*, juvenile specimens of which are not available for comparison.

Ehrenbaum also reexamined Lütken's specimens because the drawings in his paper show the first dorsal ray as very short, which led Kishinouye (1923) to doubt that they are tunas at all. From this reexamination Ehrenbaum concluded that the fin rays had been broken and that the specimens undoubtedly are tunas (*Orcynus*). However, Ehrenbaum also found that all of Lütken's specimens were probably not of the same species:

Allerdings ist sehr bemerkenswert, dass die beiden von Lütken abgebildeten Stadien von 17 und 10 mm wahrscheinlich nicht derselben Art angehören, sondern das grössere zu der von mir hier als O. germo charakterisierten Form und das kleinere zu O. thynnus. Diese Verschiedenheit ist aus den Abbildungen allerdings nicht mehr zu erkennen.

Katsuwonus pelamis

Two specimens which, as will be shown, can be definitely identified as this species were captured, as follows: 1 specimen 21 mm. total length, from 9°22.5′ N., 85°47.5′ W., January 28, 1947; 1 specimen 44 mm. total length, from 9°10′ N., 85°20′ W., March 20, 1947. The smaller specimen is depicted in figures 4 and 5. The larger was prepared for bone study.

These specimens may be recognized easily by the relatively less deep body at a given length, and by the pigmentation of the dorsal fins. The second dorsal fin was entirely unpigmented in both specimens. The first dorsal fin of the smaller individual, as may be seen in the figures, has only a few moderately large pigment spots toward the distal ends of the rays. The same was true of the larger fish but it had, in addition, some pigment along the anterior edge of the fin to the base.

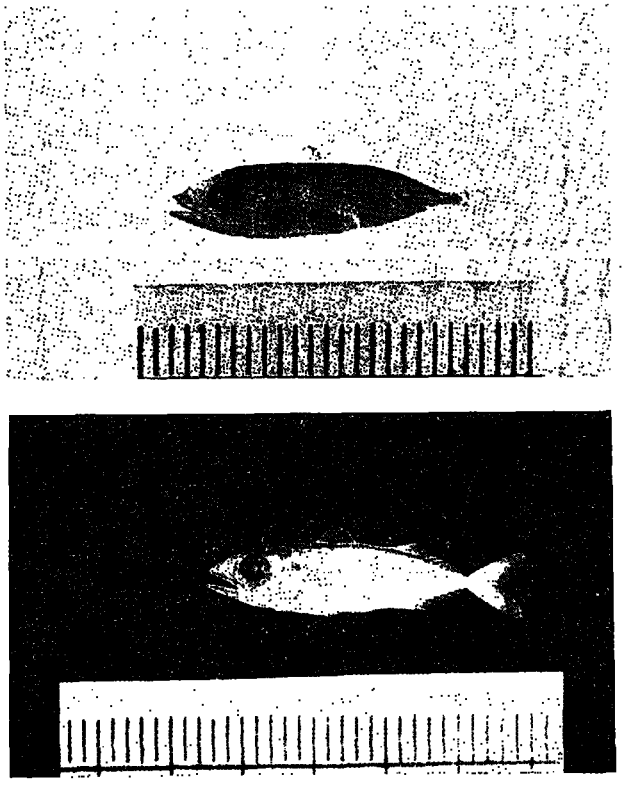

FIGURE 4.—Juvenile *Katsuwonus pelamis* photographed against light and dark backgrounds.

The smaller fish, as may be seen, is unpigmented on the belly; scattered pigment spots appear on the sides at about the level of the pectoral fin and become more concentrated dorsally. The concentration laterally is rather even, and there is no suggestion of bars on the sides. The dorsal and lateral pigmentation extends on the caudal peduncle to the bases of the caudal rays. There is a conspicuous series of black spots along the bases of the anal fin and following finlets. The posterior part of the top of the head forward of the nape is very dark; this is actually subcutaneous pigment on the brain covering. The snout and both jaws bear rather conspicuous dark pigmentation. There is a light pigmentation of the operculum, and the posterior margin of the orbit is rather dark. The larger specimen had essentially the same pigmentation except that it was heavier, and the whole dorsal part of the head was dark. No bars were present on the sides as in *Neothunnus*. The peritoneum dorsally is quite heavily pigmented, but is light below.

The 21-mm. specimen has two fairly conspicuous spines at the corner of the preopercle, preceded by a tiny spine on the inferior margin. There might be more small spines discernible at a smaller size. The spines have entirely disappeared in the 44-mm. specimen.

The vertebrae, examined in the 44-mm. specimen stained with alizarin, number 20+21, counting the urostyle. Haemal spines are present on some precaudal as well as on the caudal vertebrae. The inferior foramina are large and well developed in precaudal vertebrae 14 to 20, as well as on the anterior caudal vertebrae. The haemal canal is very large. The inferior foramina and large haemal arches form what Kishinouye calls the "trellis" and Godsil and Byers call a "complex basket work." The first closed haemal arch is found on the twelfth vertebra. The lateral processes on the posterior caudal vertebrae are fairly well developed; there are no lateral processes on the anterior precaudal vertebrae.

The pectoral fin has 26 rays. The first dorsal fin has 16 spines, the second being the longest in both our specimens. Spines following the second decrease in length successively; the first spine is longer than the fourth. The first dorsal extends to the insertion of the second. The combined count of second dorsal rays and dorsal finlets is 23. There are, apparently, eight dorsal finlets, but here again it is not easy to decide between the last ray of the fin and the first finlet. The anal consists of 15 rays and 7 finlets; the combined count is accurate but the segregation of rays and finlets may be one in error. In our 21-mm. specimen the finlets are joined to one another and to the fin by a membrane extending almost to their tips. This has entirely disappeared in the 44-mm. specimen, except between the fin and the first finlet behind the fin. The intestine passes posteriorly along the right side of the body cavity and is not folded in either specimen. The left lobe of the liver is much longer than the other two lobes, extending about half the length of the body cavity, and is somewhat attenuated distally. The anterior portion of the lateral line is visible in the larger specimen and has a gentle curve over the pectoral fin, rather than the sharp dip of the Thunnidae. The gill rakers on the first arch of the smaller specimen are short and tiny; they appear numerous, but cannot be accurately counted. In the large specimen the gill rakers on the first arch were counted as 8+33.

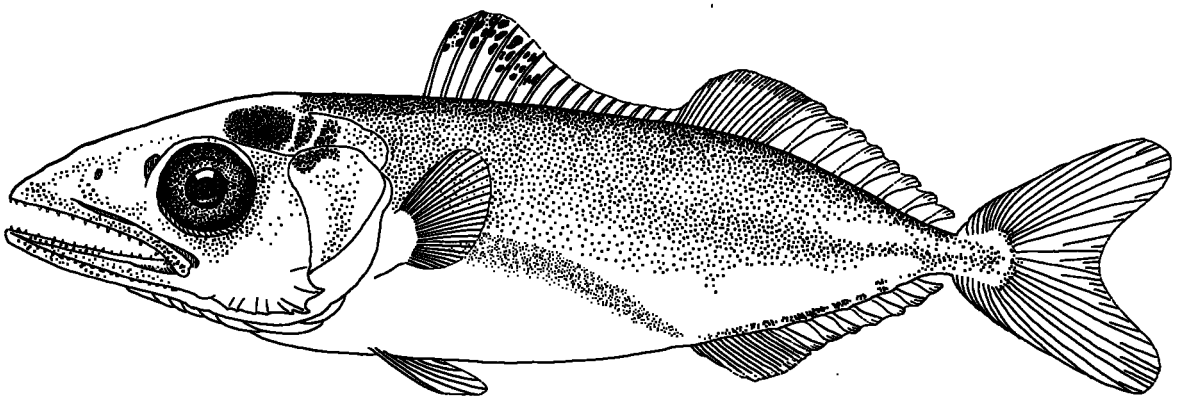

FIGURE 5.—*Katsuwonus pelamis*, 21 millimeters long.

The characteristics of the vertebral column, as described, are sufficient to identify these specimens as belonging to the "Katsuwonidae" of Kishinouye (1923), and other characters agree, such as the relative size of the liver lobes and shape of lateral line. Of the Katsuwonidae the only known species having 20+21 vertebrae is *K. pelamis*. This character alone is sufficient to identify these specimens beyond any doubt (Kishinouye 1923; Godsil and Byers 1944; Frade and deBuen 1932), and numerous other characters are in agreement.

Ehrenbaum (1924) described specimens of *Euthynnus pelamis* L.(=*Katsuwonus pelamis*) up to 10 mm. in length, the larger of which could be identified with fair certainty by the vertebrae counts as belonging to this species. Since these specimens were all much smaller than ours, we cannot verify their identification by comparison of his descriptions with specimens of similar sizes. So far as our material is comparable, however, there seems to be no reason to doubt the correctness of Ehrenbaum's identification. It appears that the light pigmentation of the first dorsal fin of our specimens was characteristic of his smaller ones also.

DISCUSSION

The observation of sexually maturing and of spent adults of *Neothunnus macropterus* and *Katsuwonus pelamis*, and the capture of juveniles of these species during the late winter and spring months in the oceanic waters off Central America, demonstrate the existence of a spawning area of these species in that vicinity at that time of year. That the juveniles were probably moderately numerous in this region may be inferred from the fact that, out of 17 stations off Costa Rica and northern Panama at which we captured organisms under a drop light between January 28 and May 7, we took *Neothunnus* at 4 stations, of which 2 also furnished specimens of *Katsuwonus*. Three of these four stations were off Costa Rica and one off Panama. From these scattered observations no conclusions regarding the geographic concentration or extent of occurrence of juveniles can be drawn.

Although this region is now the only definitely known spawning area of yellowfin tuna and skipjack in the eastern Pacific, these species both have wide ranges, and it would be highly desirable to investigate other areas in order to determine over what part of the total ranges spawning occurs.

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SIZE COMPOSITION OF CATCHES OF YELLOWFIN TUNA (*NEOTHUNNUS MACROPTERUS*) FROM CENTRAL AMERICA, AND THEIR SIGNIFICANCE IN THE DETERMINATION OF GROWTH, AGE, AND SCHOOLING HABITS

By Milner B. Schaefer

The factory ship *Pacific Explorer* was employed during the late winter and spring months of 1947 in collecting and freezing a cargo of tuna, mostly yellowfin, from Pacific waters adjacent to Costa Rica. Aboard the vessel were biologists of the Fish and Wildlife Service until mid-May (the author until mid-March when relieved by J. C. Marr). It was possible for us to examine the catches of the accompanying fishing boats, both at sea as they were being made and aboard the mother ship. Among the data gathered on the biology of the yellowfin tuna were a series of length-frequency samples of the catches. These shed some light on the age and growth, and on the manner of aggregation into schools.

COLLECTION OF DATA

Most fish in the samples were measured at sea as caught, and the sample from each school was kept separate. When less than 50 fish were caught from a school, ordinarily the entire catch was measured. When more than 50 fish were caught, a minimum of 50 fish were taken at random from the catch and measured. In a few cases, samples from catches were measured when the fish were landed aboard the mother ship. In such cases, the samples were usually from several schools combined.

The total length of the fish, from the tip of the snout to the fork of the tail, was measured with a large pair of slide calipers.[1] In making this measurement, one arm of the calipers was seated firmly against the tip of the snout and the other against the cartilaginous tissue in the fork of the tail.

In addition to the measurements made in the field on freshly caught fish, two landings of fish taken in the waters off Costa Rica during the last week in June and landed aboard the *Pacific Explorer* were sampled when unloaded at Astoria (Oreg.) in mid-July. These were measured at the cannery of Columbia River Packers, Inc., after being thawed in vats of water preparatory to butchering for canning.

In figure 1, we have summarized the data for *Neothunnus macropterus* (Temminck and Schlegel), the yellowfin tuna, by three periods. The upper length-frequency graph represents fish measured from January 27 to February 8. Included are 233 fish from the individual schools which are graphed by separate schools in figure 2, plus 118 other fish, consisting of 62 from four individual schools and 56 drawn at random from two landings of mixed schools which were landed aboard the mother ship. All these fish were taken by bait boats. The middle graph of figure 1 includes the following fish taken between March 20 and April 24: 184 fish caught by bait boats and 100 fish caught by purse seiners, graphed by individual schools in figure 3, plus 47 other fish taken by bait boats from four other individual schools and 10 fish drawn at random from a bait-boat landing on the mother ship. The bottom graph in figure 1 includes samples of fish from each of two landings aboard the mother ship; these fish, which total 199, were caught in each instance by bait boats from waters off Costa Rica. These two samples were measured after the frozen fish had been thawed at the cannery. They are presumed to include representatives from several schools.

In all the graphs the fish, which were measured to the nearest millimeter, have been grouped by two-centimeter length classes, each class including the millimeters from zero to nine in an odd centimeter and the following even centimeter. The class intervals are, thus, for example, 610 mm. to 629 mm., 630 mm. to 649 mm., etc., with mid-points 619.5 mm., 639.5 mm., etc.

AGE AND GROWTH

Some inferences as to age and growth can be made from the modes in figure 1. The youngest group, near 60 cm., is represented by only scattered individuals in the bait-boat catches of the first two periods,

[1] The calipers used were very kindly loaned to us by H. C. Godsil of the California State Fisheries Laboratory.

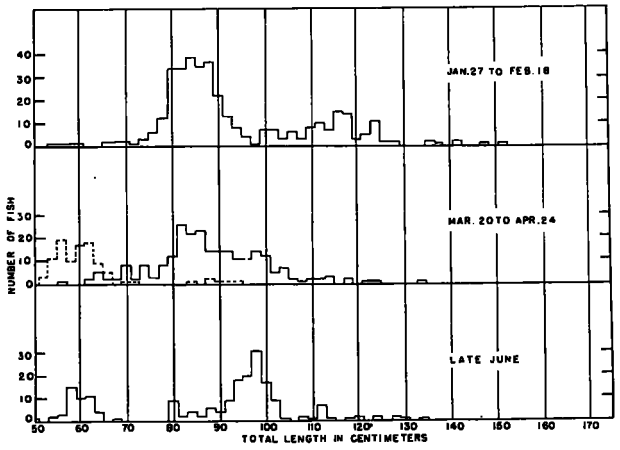

FIGURE 1.—Length frequencies of samples of yellowfin-tuna catches, summarized by periods, 1947. (Solid line, bait-boat catches; broken line, purse-seine catches.)

but is well represented in the June samples. This group also made up the major part of the two purse-seine catches sampled. The difference in the size composition of the catches of bait boats and seiners in March and April appears to the author to be primarily a matter of the selectivity of the bait fishing. During cruises on bait boats in these waters, we saw large numbers of small yellowfin, very often schooled with skipjack, *Katsuwonus pelamis* (Linnaeus), of similar size, but they did not respond to the methods of the bait fishery. The modal size of this group in the population may not be accurately reflected in the corresponding modes in the samples, both because of the schooling habits of the fish and because of the probable selectivity of the fishing methods. The fish in this group are probably the one-year-olds, although it is possible that they are the two-year-olds. This conclusion is based on the relation of the position of this mode to the next, that at 85 cm. in the January-February samples, which is presumed to be composed primarily of fish a year older than this smallest group. The fish in the smallest group were completely immature in all samples, while those of larger sizes were nearly all undergoing maturation of the gonads in the samples taken through April, many of them being very close to spawning as judged by the presence of large, opaque, yolk-laden ova in many of the females, and the presence of running milt in the ducts of the testes of some males. These larger sizes among the fish taken in late June were spent fish, some apparently rather recently so.

Although little progression of the mode of the smallest fish is evident, there appears to be a progressive increase in the size of the fish making up the second mode. This may be spurious, however. Tracing the growth over such a short period by means of progression of modes of size frequencies is made difficult by the tendency of the fish to school by sizes, with the attendant sampling errors, which will be discussed in more detail later.

It is not possible to trace the growth of the fish beyond the second year by means of these length frequencies. The mode near 115 cm. in the first period in figure 1 is very likely composed of fish of more than one age group. Even the second mode may contain fish of more than one age. In a longer series, however, made up of samples of more schools, it may prove possible to identify older age groups by means of size frequencies.

It seems probable from these data that the yellowfin tuna of the Pacific off Central America grow at a very rapid rate, and that the bulk of the catch is made up of members of relatively few year classes, a considerable number of fish caught being probably only 1 year old.

The rapid rate of growth of these tunas, inferred from the length frequencies, agrees with the findings of other authors regarding yellowfin and bluefin tunas from other parts of the world. Kishinouye (1923) says,

> The growth of tunnies seems to be very rapid. The common tunny, *Thunnus orientalis*, most probably reaches maturity in the third year of age. *Thunnus orientalis*, ca 22 cm. in the total length, is the smallest specimen I have seen * * * such small individuals are found in August and in September. Some of them grow to a length of 30 cm. or more. By next spring they grow to a length of ca 60 cm. When 2 years old they are about 1 metre in length and 11 kg. in weight * * * The growth of *Thunnus germo* and *Neothunnus macropterus* in the first and second years seems to be nearly the same as that of the common tunny * * *.

Sella (1929) states that tuna (*Thunnus thynnus*) hatched in May and June in the Mediterranean weigh 300 to 500 grams in September. He has determined the ages of fish of this species by marks on the vertebrae, and gives the following average sizes at various ages:

Age	Length in centimeters	Weight in kilos
1	64	4.4
2	81.5	9.5
3	97.5	16
4	118	25
5	136	40
6	153	58
7	169	76

Westman and Neville (1942) have been able to determine the ages of *Thunnus thynnus*, from waters off New York, by length frequencies up to three years of age and by scale readings for those and also older ages. They state:

> In the July 1–15 sample, the fish between 20 and 24 inches [50 and 60 cm.] were in their second summer of growth; those between 27 and 34 inches [68 and 86 cm.] were in their third summer; those between 35 and 40 inches [88 and 101 cm.] were in their fourth summer; and those between 42 and 46 inches [106 and 116 cm.] were in their fifth summer of growth.

The metric values in brackets have been inserted by the author. Westman's and Neville's figure 9 shows the following approximate positions of the modes of size groups in the length frequencies of August and September caught fish: 1-year-olds, 60 cm.; 2-year-olds, 85 cm.; and 3-year-olds, 105 cm.

SCHOOLING HABITS

In figures 2 and 3 we have graphed, by separate schools, those samples of yellowfin tunas which were drawn from individual schools, and which were large enough to characterize the size composition of the school. It is quite evident from the figures that each school is not a random aggregation of members from the whole population of the area, but that there is a distinct tendency for fish of the same size to school together. The members of any given school are more nearly of the same size than would be expected if they were merely drawn at random from the whole population. The degree to which fish of a school tend to be of the same size varies between schools. The school sampled on January 29, for example, was composed of fish of rather uniform size, while the one sampled on February 3 was a mixture of a larger range of sizes.

The tendency to aggregate by similar sizes may be, in some cases, stronger than the tendency to aggregate by species. As stated previously, the small, 1-year-old yellowfin, during the period of our observation, very often were seen schooled with skipjack of about the same size, rather than with larger fish of their own species. The purse seine catch sampled on March 28 was from a single mixed school of this sort. The size distributions of the samples of each of the two species in this catch are shown in figure 4; the similarity of sizes of the two species in this school is obvious.

The tendency of the tunas to school by sizes has important implications in the design of any sampling program for determining the size composition of the population. In order that the size composition of the total sample be representative of the size composition of the population it is necessary that the different strata of the population—in this case types of schools—be each represented in proportion to the

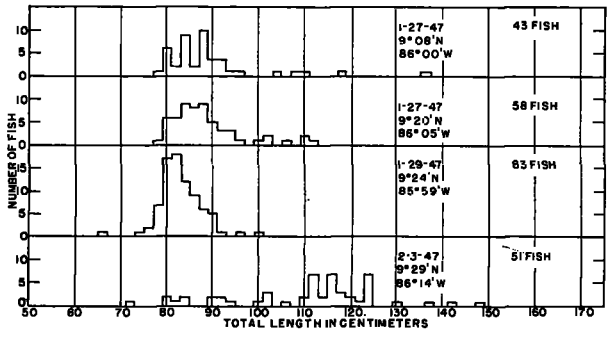

FIGURE 2.—Length frequencies of samples of yellowfin tuna from individual schools, caught by a bait boat in late January and early February 1947.

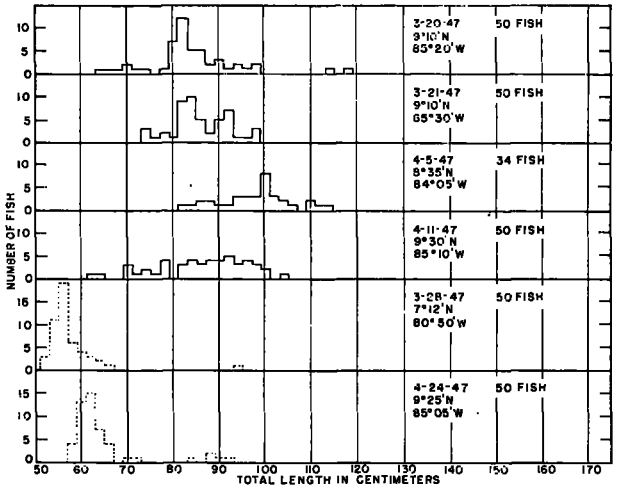

FIGURE 3.—Length frequencies of samples of yellowfin tuna from individual schools, caught by bait boats (solid line) and purse seiners (broken line) in March and April 1947.

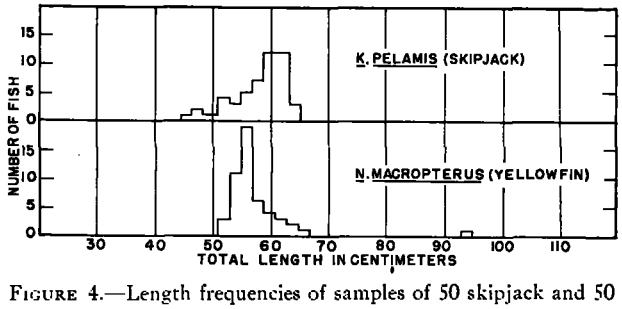

FIGURE 4.—Length frequencies of samples of 50 skipjack and 50 yellowfin from a mixed school caught by purse seine near 7°12′ N. 80°50′ W. on March 28, 1947.

number of members in the stratum. It would seem desirable, since we know that the population is grouped into schools by sizes, that the school be made the basic unit of sampling. That is, it is desirable that the total sample be composed of subsamples drawn by either representative or random methods from each of a large number of schools selected randomly from the population. A large number of fish drawn from only a few schools will not likely be as representative of the population as the same number drawn a few each from a large number of randomly chosen schools. Our own samples suffer from a lack of being drawn from a sufficient number of schools to give a very reliable estimate of the positions of the modes in the population at large. As a consequence, the interpretation of the length frequencies of figure 1 lacks precision; it is possible to determine only roughly the size frequencies in the population from the frequencies in these samples.

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OBSERVATIONS ON THE SPAWNING OF OCEANIC SKIPJACK (*KATSUWONUS PELAMIS*) AND YELLOWFIN TUNA (*NEOTHUNNUS MACROPTERUS*) IN THE NORTHERN MARSHALL ISLANDS

By John C. Marr [1]

A spawning area of the oceanic skipjack, *Katsuwonus pelamis* (Linnaeus 1758), and the yellowfin tuna, *Neothunnus macropterus* (Temminck and Schlegel 1850), off the Pacific Coasts of Costa Rica and Panama has been recorded, on the basis of the examination of gonads of adult fishes and the capture of juveniles, by Schaefer and Marr (p. 187). No other spawning localities of these species have been recorded in the Pacific, although Matsui (1942), on the basis of the relation of gonad weight to body weight in *Katsuwonus* taken near Japan and near Palau, concluded that those taken near Palau were more mature than those from Japanese waters and that a spawning region might exist in the vicinity of Palau. (I have not seen this paper; the above is based on an abstract of it by Yoshio Hiyama.)

From March to August 1946, and in July and August 1947, I was detailed to duty with the United States Navy in the northern Marshall Islands area. My duties were largely concerned with studies of the biology of the pelagic fishes, particularly in the vicinity of Bikini, Rongerik, and Rongelap Atolls in 1946, and Bikini and Rongerik Atolls in 1947. On the basis of examinations of the gonads of adults of these 2 species, it seems probable that spawning occurs in or near this region. This is confirmed for *Katsuwonus pelamis* by the incidental capture of 2 juveniles. No other juveniles were taken, since virtually no collecting was done in the open sea where spawning probably takes place. All adult specimens examined were taken by trolling feather or bone jigs in the open sea or adjacent to the atolls, never in the lagoons. Large yellow-fin tuna carried away the gear employed, and the larger sizes are not represented in the catch. The oceanic skipjack did not do this, since they do not attain such large sizes, and the catch should be representative of the sizes present in the area or, at least, in the schools fished.

The degree of sexual maturity of the fishes of all species taken was evaluated for as many fishes as possible. It was not possible to do this for all fishes in 1946 due to the lack of personnel; it was done for almost all fishes taken during 1947. Some of the 1946 observations were made by commercial fishermen who had been trained to distinguish between the different stages of maturity; the 1947 observations were made by biologists. When the visceral cavity of the fish was opened to determine the sex, the degree of maturity of the gonads was classified as follows: immature, ripening, ripe, spawning, or spawned out.

Gonads not at all enlarged, merely a small, ribbon-like body, were classified as immature. Without microscopic examination, it is difficult to distinguish males from females at this stage and some sex determinations may be in error. Ovaries, which are tubular, may often roll between the fingers (as would a piece of glasss tubing) and the opposite walls of the ovary may be felt sliding over each other. Testes, which are solid and not round in cross section, do not roll but turn over between the fingers (as would an object which is angular in cross section) and the opposing walls do not slide over each other.

Ripening gonads are somewhat enlarged, but not fully ripe. No difficulty is experienced in determining the sex at this stage; ovaries are enlarged, turgid bodies, round in cross section; testes are solid, pinkish bodies not round in cross section.

Ripe gonads are greatly enlarged. The ova are distinguishable by the naked eye and may be easily dislodged. The testes are whitish and often have milt in the central duct. For *Katsuwonus* and *Neothunnus* no running-ripe individuals were noted and this stage might be more properly termed "ripening, advanced" for there is a possibility that the gonads of *Katsuwonus*, at least, remain in this enlarged state some time before spawning actually takes place. However, in the present data this situation can not be distinguished from one in which the actively spawning individuals are present in the area but not present in the catch.

Gonads classified as "spawning" have the same general characteristics as the "ripe" gonads, but the

[1] Valuable field assistance was rendered in this work by M. A. Traylor, Chicago Natural History Museum, in 1946, V. E. Brock, Director, Division of Fish and Game, Territory of Hawaii, in 1946 and 1947, and Dr. Osgood R. Smith, of the Fish and Wildlife Service, in 1947.

sexual products may in some cases be expressed by external pressure. Ovaries may appear to be partially emptied. This latter criterion was most often employed for these two species.

Spawned out ovaries are hollow, more or less flabby, sac-like tubes. Testes at this stage are pinker, tougher, and less turgid than those which are ripening, but it is often difficult to distinguish between these two stages in males.

The methods employed are somewhat subjective, but are exact enough to permit the detection of major changes such as would be brought about by a spawning season. Data on approaching maturity and time of spawning are probably more reliable for females than for males.

KATSUWONUS PELAMIS (LINNAEUS 1758)

In 1946, a total of 144 skipjack were taken between April 3 and August 14. Of these, information on sex and degree of maturity are available for 107; length data are available for 143. In table 1 are given the dates of capture, locality, fork length (the straight line distance from the tip of the snout with the jaws closed to the end of the cartilage, with the small fleshy flap depressed, in the median part of the caudal fork), sex, and degree of maturity for the 107 fish mentioned. The following fish were considered to be immature: males, 451 mm., July 26; 467 mm., July 29; 661 mm., August 7; females, 457 mm. August 3; 443 mm., August 9; 444 mm., August 9. The females and all but one of the males are all in the lower end of the size-range covered by the catch. From April 11 to August 13, 98 males and females were considered to be ripe. Among these fish are included some that probably should have been classified as ripening and some of the males may have been spawned out. The following fish, all females, were found to be spawned out: 611 mm., April 22; 673 mm., July 20; 453 mm., July 26.

These data might be interpreted as indicating that the oceanic skipjack spawn in or near this area, but most of them at some time after the date upon which the last fish was examined. An alternative explanation is that the spawning season falls within the period covered by field work, but that the spawning and spawned out fish were largely unavailable to the fishery (this would include the possibility that large-scale spawning takes place during the entire year).

In 1947, a total of 84 skipjack were taken between July 19 and August 22. Of these, information on sex and degree of maturity are available for 72; length data are available for 80. Table 1 includes these and other data. During this period no fish were judged to be immature. From July 23 to August 21, 15 fish were considered to be ripening. All but one of these are males and some may have been spawned out fish that were mis-classified. A total of 46 fish were considered to be ripe. A total of 11 fish were classified as spawning or spawned out. The first of these was taken on July 29 and the remainder were taken on or after August 12.

The 1947 data support conclusions similar to those drawn from the 1946 data. There is, perhaps, a little more evidence to indicate that the spawning season is actively under way in August.

Ovaries that were classified as ripe, from two skipjack taken on July 24, 1947, were preserved in formaldehyde. Subsequent examination indicates that a small percentage of the ova may have been spawned before the fish were caught; i. e., the most posterior portions of the ovaries were partially hollow, resembling the condition of ovaries that were considered to be spawned out. Ova from the posterior portion of these ovaries were measured with an eyepiece micrometer under a compound microscope. In an ovary of one fish the largest ovum measured had a diameter of 0.65 mm. This ovum was associated with a mode centering at 0.53 mm. Two other size groups were present, one centering at 0.35 mm. and the other at 0.18 mm. Similar size-groups of ova with perhaps slightly smaller modal diameters were present in an ovary of the other fish. This suggests that the ova are spawned in batches. Fractional spawning has been demonstrated in *Thunnus thynnus* (Linnaeus) by Fradé and Manaças (1933) and suggested in *Neothunnus macropterus* by Schaefer and Marr (p. 188). The largest ova are probably approaching full size. According to Schaefer and Marr "Ova from a preserved ovary of a running-ripe *Euthynnus lineatus* Kishinouye from Costa Rica measure 0.72 to 0.81 mm. in diameter." Sanzo (1929) gives 1.0 mm. to 1.2 mm. as the diameter of the fertilized ova of *Thunnus tyhnnus*. It is to be expected that oceanic skipjack ova would increase in diameter after emission into sea water.

On July 24, 1947, several fishes were regurgitated by adult *K. pelamis* taken off the northwest end of Bikini Atoll (3 miles west of Bokobyaadaa Island). Among these fishes are 2 juvenile scombroids between 45 mm. and 50 mm. in length, partially digested and distorted. These have been identified as *Katsu-*

TABLE 1.—*Length, sex, and degree of maturity data for Katsuwonus pelamis taken in the northern Marshall Islands during 1946 and 1947*

Date	Locality	Length in millimeters	Sex	Degree of maturity
1946				
Apr. 11	Bikini	634	Female	Ripe.
15	do	498	do	Do.
20	Rongerik	620	Male	Do.
20	do	571	do	Do.
21	do	619	do	Do.
21	do	617	do	Do.
22	do	608	do	Do.
22	do	611	Female	Spawned out.
23	do	628	do	Ripe.
23	do	619	do	Do.
May 13	do	488	do	Do.
14	do	570	do	Do.
18	Rongelap	498	Male	Do.
18	do	491	Female	Do.
22	Bikini	675	Male	Do.
31	Rongelap	628	Female	Do.
June 1	do	625	do	Do.
19	Bikini	514	do	Do.
25	Rongelap	629	Male	Do.
July 3	do	470	Female	Do.
3	do	470	do	Do.
8	Bikini	684	Male	Do.
8	do	680	do	Do.
8	do	686	do	Do.
8	do	672	do	Do.
9	do	667	do	Do.
9	do	669	do	Do.
9	do	659	Female	Do.
9	do	660	Male	Do.
9	do	655	Female	Do.
9	do	703	do	Do.
9	do	661	Male	Do.
9	do	680	do	Do.
9	do	665	Female	Do.
9	do	640	do	Do.
9	do	691	Male	Do.
9	do	691	do	Do.
9	do	666	do	Do.
9	do	687	do	Do.
9	do	653	Female	Do.
9	do	692	Male	Do.
9	do	654	do	Do.
9	do	661	Female	Do.
9	do	691	Male	Do.
9	do	667	do	Do.
9	do	684	do	Do.
9	do	657	Female	Do.
20	Rongerik	638	Male	Do.
20	do	673	Female	Spawned out.
23	do	629	Male	Ripe.
26	Rongelap	453	Female	Spawned out.
26	do	451	Male	Immature.
29	Ailinginae	454	do	Ripe.
29	do	444	do	Do.
29	do	467	do	Immature.
Aug. 2	Bikini	654	do	Ripe.
2	do	651	Female	Do.
2	do	658	Male	Do.
2	do	628	Female	Do.
2	do	678	Male	Do.
2	do	688	do	Do.
2	do	659	do	Do.
3	do	457	Female	Immature.
3	do	647	Male	Ripe.
3	do	684	do	Do.
3	do	454	Female	Do.
3	do	454	Male	Do.
5	do	500	do	Do.
5	do	500	do	Do.
5	do	463	Female	Do.
5	do	435	Male	Do.
5	do	459	Female	Do.
5	do	496	Male	Do.
5	do	463	Female	Do.
5	do	506	Male	Do.
5	do	478	Female	Do.
5	do	483	Male	Do.
5	do	454	do	Do.
5	do	480	Female	Do.
5	do	470	Male	Do.
5	do	459	Female	Do.
5	do	477	Male	Do.
5	do	448	do	Do.
5	do	463	do	Do.
5	do	479	do	Do.
7	do	450	do	Do.
7	do	661	do	Immature.
7	do	668	do	Ripe.
7	do	431	do	Do.
7	do	489	Female	Do.
7	do	451	Male	Do.
1946				
Aug. 7	Bikini	460	Female	Ripe.
7	do	698	Male	Do.
7	do	644	Female	Do.
9	do	448	Male	Do.
9	do	443	Female	Immature.
9	do	439	do	Ripe.
9	do	442	Male	Do.
9	do	448	do	Do.
9	do	455	do	Do.
9	do	450	do	Do.
9	do	391	do	Do.
9	do	444	Female	Immature.
10	do	683	Male	Ripe.
10	do	654	Female	Do.
10	do	549	Male	Do.
13	do	664	do	Do.
1947				
July 19	do	588	do	Do.
23	do	672	do	Ripening.
24	do	543	Female	Ripe.
24	do	540	do	Do.
24	do	535	do	Do.
24	do	570	Male	Do.
24	do	547	Female	Do.
24	do	542	Male	Do.
24	do	514	Female	Do.
24	do	565	do	Do.
24	do	552	do	Do.
24	do	560	do	Do.
24	do	532	Male	Do.
24	do	598	Female	Do.
24	do	565	Male	Do.
24	do	488	Female	Do.
24	do	504	Male	Do.
24	do	488	Female	Do.
24	do	574	Male	Do.
24	do	598	Female	Do.
24	do	470	Male	Do.
24	do	544	Female	Do.
24	do	----------	Male	Do.
24	do	475	do	Do.
24	do	545	do	Do.
24	do	460	do	Ripening.
26	do	598	do	Ripe.
26	do	732	do	Do.
28	do	482	do	Ripening.
28	do	572	do	Ripe.
28	do	461	Female	Ripening.
28	do	488	do	Ripe.
28	do	720	Male	Do.
28	do	718	do	Do.
29	do	656	do	Do.
29	do	698	do	Do.
29	do	642	do	Do.
29	do	407	Female	Spawned out.
30	do	458	Male	Ripening.
30	do	463	do	Do.
30	do	436	Female	Spawning or spawned out.
31	do	441	do	Ripe.
31	do	460	Male	Ripening.
31	do	432	do	Ripe.
31	do	467	Female	Do.
31	do	559	Male	Do.
31	do	453	do	Ripening.
Aug. 2	do	449	do	Ripe.
2	do	447	do	Do.
2	do	465	do	Do.
5	do	470	do	Ripening.
6	do	452	do	Do.
8	do	437	do	Ripe.
8	do	430	do	Ripening.
8	do	448	do	Ripe.
12	Rongerik	455	do	Ripening.
12	do	468	do	Do.
12	do	442	Female	Spawned out.
12	do	463	do	Do.
12	do	464	Male	Ripening.
13	do	675	Female	Spawning.
13	do	481	do	Do.
13	do	475	do	Spawned out.
14	do	450	Male	Ripe.
14	do	664	Female	Do.
20	do	459	Male	Do.
20	do	682	Female	Spawned out.
21	do	465	do	Spawning.
21	do	465	Male	Ripening.
22	do	463	do	Ripe.
22	do	482	Female	Spawned out.
22	do	459	do	Spawning.

wonus pelamis. One of these specimens was stained and cleared for study of the bony parts, using the methods described by Hollister (1934). The "complex basketwork" formed by the haemal arches and inferior foramina is characteristic of *Katsuwonus* and *Euthynnus* (Kishinouye 1923; Godsil and Byers 1944). That these specimens are *Katsuwonus* is indicated by the presence of 41 vertebrae. The gill rakers on the most anterior gill arches of both specimens were counted as 6+32. The full complement of rakers has probably not yet been attained. Gill-raker counts of adult *K. pelamis* taken in the same area are 16–21+33–40 and of *Euthynnus yaito* (Kishinouye 1915) are 8–10+23–26. This further indicates that the specimens are *K. pelamis*, rather than *E. yaito*. It is of interest to note that palatine teeth are present, although the absence of these teeth is supposedly characteristic of *Katsuwonus*. This is undoubtedly true of the adults. Reexamination of the 21-mm. specimen described by Schaefer and Marr (p. 193) disclosed that palatine teeth are present. These teeth are probably grown over by the time the fish attain adult sizes. A similar situation has been noted in *Auxis thazard* (Lacépède 1802) by Schaefer and Marr.

The dates on which juvenile oceanic skipjack were collected in Central American waters by Schaefer and Marr (p. 189) indicate that spawning takes place in those waters, at least, from January into March. Further, six adults examined by them on February 21, 1947, were maturing; one male and one female were nearly ready to spawn. Ten adults examined by them on March 30, 1947, appeared to be spawned out. Ehrenbaum (1924: 33) records juvenile *Euthynnus pelamis* (=*K. pelamis*) under 10 mm. in length taken in the Atlantic Ocean and the Arabian Sea from July to December. Chapman (1946: 169) took young "skipjack" 8 to 10 inches long between Guadalcanal and Florida Island. However, it is not clear whether he refers to *E. yaito* or *K. pelamis* or both. Kishinouye (1923: 456) believed the spawning season to be from May to August, although the basis for his belief was not given. From the above it would seem that oceanic skipjack either spawn throughout the year in all spawning localities or that the time of spawning varies from locality to locality. The presence of modal size-groups in the catch in the northern Marshall Islands favors the latter alternative.

Ripe gonads were found over the entire size-range of northern Marshall Island fish examined for degree of maturity. The upper panel in figure 1 shows the length-frequency distributions for the oceanic skipjack taken in 1946 and 1947, including individuals for which information on the degree of maturity is not available.

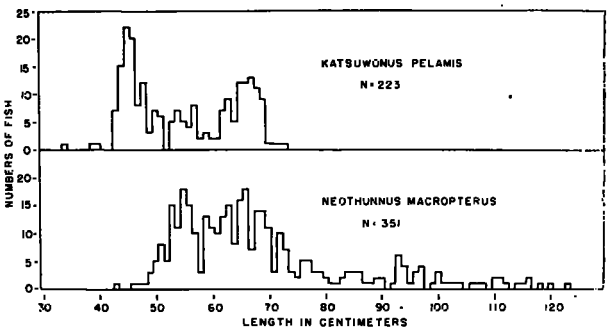

FIGURE 1.—Length frequency distributions of oceanic skipjack and yellowfin tuna taken in the northern Marshall Islands during 1946 and 1947.

NEOTHUNNUS MACROPTERUS (TEMMINCK AND SCHLEGEL 1850)

In 1946, a total of 284 yellowfin tuna were taken between April 1 and August 14. Of these, information on sex and degree of maturity are available for 101; length data are available for 280. In table 2 are given the dates of capture, locality, fork length, sex, and degree of maturity for the 101 fish mentioned The observations recorded on July 29, August 4, 5, and 7 were made by an inexperienced observer and should be regarded as extremely questionable. They are not included in the following discussion. Of the remaining 91 fish, 64 were considered to be immature. These are all in the lower end of the size range covered in the catch. The following fish were classified as ripening: males; 925 mm., April 20; 660 mm., April 20; 768 mm., June 15; females: 943 mm., April 20; 856 mm., April 21; 992 mm., April 21; 663 mm., April 22; 718 mm., April 24; 716 mm., June 2; 965 mm., August 14. A total of 16 fish were considered to be ripe. These were taken between May 16 and July 26. The smallest was 741 mm., and all but 6 were longer than 900 mm. One female, 1,144 mm., taken on April 20, was considered to be spawned out.

It has been shown by Schaefer and Marr (p. 187), that among the yellowfin examined off Costa Rica in January and February, the fish more than 1,000 mm. in length were in advanced stages of sexual maturity. This was not true for fish under this length. However, by April many of the fish down to 700 mm. had

TABLE 2.—*Length, sex, and degree of maturity data for Neothunnus macropterus taken in the northern Marshall Islands during 1946 and 1947*

Date	Locality	Length in millimeters	Sex	Degree of maturity
1946				
Apr. 1	Bikini	683	Female	Immature.
1	do	645	do	Do.
1	do	643	do	Do.
1	do	595	do	Do.
1	do	613	Male	Do.
1	do	528	do	Do.
1	do	550	do	Do.
2	do	588	do	Do.
2	do	626	do	Do.
6	do	694	do	Do.
15	do	745	do	Do.
15	do	693	Female	Do.
15	do	653	do	Do.
15	do	647	do	Do.
15	do	572	Male	Do.
17	do	872	Female	Do.
17	do	704	Male	Do.
17	do	728	do	Do.
20	Rongerik	1,144	Female	Spawned out.
20	do	672	do	Immature.
20	do	925	Male	Ripening.
20	do	611	do	Immature.
20	do	637	do	Do.
20	do	593	do	Do.
20	do	615	do	Do.
20	do	943	Female	Ripening.
20	do	619	Male	Immature.
20	do	660	do	Do.
20	do	660	do	Ripening.
21	do	856	Female	Do.
21	do	992	do	Do.
21	do	509	Male	Immature.
21	do	527	do	Do.
22	do	752	Female	Do.
22	do	578	Male	Do.
22	do	626	do	Do.
22	do	684	do	Do.
22	do	801	do	Do.
22	do	634	Female	Do.
22	do	663	do	Ripening.
22	do	634	Male	Immature.
24	do	667	do	Do.
24	do	632	do	Do.
24	do	685	Female	Do.
24	do	676	do	Do.
25	do	718	do	Ripening.
May 16	Rongelap	1060	do	Ripe.
16	do	1178	do	Do.
16	do	1095	Male	Do.
16	do	1160	do	Do.
16	do	1005	do	Do.
17	do	721	Female	Immature.
17	do	504	do	Do.
17	do	784	do	Do.
18	do	995	do	Ripe.
18	do	967	do	Do.
18	do	702	Male	Immature.
June 1	Rongerik	683	Female	Do.
2	do	716	do	Ripening.
4	Rongelap	1000	do	Ripe.
4	do	842	Male	Do.
4	do	692	Female	Immature.
4	do	898	Male	Ripe.
4	do	741	do	Immature.
4	do	778	Female	Ripe.
4	do	717	Male	Immature.
4	do	695	do	Do.
11	Bikini	585	Female	Do.
13	do		Male	Do.
13	do		Female	Do.
13	do		do	Do.
15	do	851	Male	Do.
15	do	768	do	Ripening.
15	do	686	do	Immature.
24	Rongelap	658	do	Do.
July 3	do	1204	Female	Ripe.
3	do	970	do	Do.
3	do	625	Male	Immature.
20	Rongerik	555	do	Do.
21	do	763	Female	Ripe.
21	do	741	do	Do.
26	Rongelap	628	Male	Immature.
1946				
July 26	Rongelap	925	Male	Immature.
26	do	601	do	Do.
26	do	593	do	Do.
26	do	621	Female	Do.
26	do	891	do	Ripe.
27	Ailinginae	773	Male	Immature.
27	Rongelap	781	Female	Do.
29	Ailinginae	668	Male	Ripe.[1]
29	do	640	do	Do.
29	do	645	do	Do.
Aug. 4	Bikini	786	Female	Do.
5	do	640	Male	Do.
7	do	652	do	Do.
7	do	527	do	Do.
7	do	654	do	Do.
7	do	635	Female	Spawned out.
7	do	669	Male	Ripe.[1]
14	do	965	Female	Ripening.
1947				
July 21*	do	544	Male	Immature.
23	do	540	do	Do.
23	do	526	do	Do.
23	do	530	do	Do.
23	do	567	do	Do.
23	do	1041	Female	Spawned out.
23	do	931	Male	Ripening.
25	do	541	Female	Immature.
26	do	611	do	Do.
26	do	666	Male	Do.
26	do	552	Female	Do.
26	do	933	do	Ripening.[2]
27	do	935	do	Spawned out.
28	do	522	Male	Immature.
29	do	600	do	Do.
29	do	839	Female	Spawned out. (Or immature?)
30	do	547	Male	Immature.
30	do	533	do	Do.
30	do	561	Female	Do.
Aug. 2	do	1078	do	Ripening.
2	do	1015	Male	Do.
7	do	943	do	Do.
12	Rongerik	547	do	Immature.
12	do	514	do	Do.
12	do	787	do	Ripening.
12	do	739	do	Immature.
12	do	661	do	Do.
12	do	546	do	Do.
13	do	655	Female	Do.
13	do	534	Male	Do.
14	do	676	do	Do.
14	do	585	do	Ripening.
14	do	549	do	Do.
14	do	525	do	Do.
14	do	536	do	Immature.
14	do	553	do	Do.
14	do	565	do	Do.
19	do	551	do	Do.
19	do	897	Female	Spawned out.
21	do	567	Male	Immature.
21	do	543	do	Do.
21	do	846	do	Do.
21	do	677	do	Ripening.
21	do	561	do	Immature.
21	do	536	do	Do.
21	do	541	Female	Do.
21	do	527	Male	Do.
21	do	533	Female	Do.
21	do	531	Male	Do.
21	do	551	do	Do.
21	do	550	do	Do.
21	do	555	do	Do.
21	do	553	do	Do.
21	do	562	do	Do.
21	do	565	do	Do.
21	do	826	Female	Spawned out.
21	do	1,103	do	Do.
21	do	726	Male	Ripening.
22	do	763	do	Immature.
22	do	837	Female	Spawned out.
22	do	552	Male	Immature.
22	do	556	do	Do.
22	do	569	do	Do.

[1] Estimate of degree of maturity probably unreliable.
[2] Microscopic examination of preserved ovary indicates that this fish was probably spawned out.

ripe gonads. Smaller fish, of a modal length of about 600 mm., were always immature during this period. By analogy, it may be inferred that a large part of the Marshall Island catch was made up of fish too small to furnish information on the time of spawning. Considering only the larger fish, ripening individuals were found from late April to mid-June and ripe individuals from mid-May to late July. This suggests that the spawning season may be in July and August or later, although one spawned-out female was taken on April 20.

In 1947, a total of 78 yellowfin tuna were taken between July 21 and August 22. Of these, information on sex and degree of maturity are available for 63; length data are available for 71. Table 2 includes these and other data. A total of 45 fish were judged to be immature and, as in 1946, these fish were all in the lower end of the size range. From July 26 to August 21, 11 fish were classified as ripening. No fish were considered to be ripe. From July 23 to August 22, 7 fish were classified as spawned out.

To check these allocations, ovaries and testes of several fish (3 ovaries classified as spawned out, and 2 ovaries and 1 testis classified as ripening) were preserved in formaldehyde and later examined under a compound microscope. The standard of comparison so obtained indicated that previous allocations had been correct, with one exception. One female, 933 mm., classified as ripening, was probably spawned out. The ovary probably never becomes as small as it was before the initial spawning, and between subsequent spawnings the stages "ripening" and "spawned out" will at some time during the cycle be identical.

The small numbers of large yellowfin in the catch in 1946 and 1947 make it difficult to define with certainty a spawning season in the northern Marshall Islands. It seems certain that some spawning does occur in the area and, if extensive, it may be concentrated in July and August and possibly later months.

The lower panel in figure 1 shows the length-frequency distribution of the yellowfin tuna taken in the northern Marshall Islands in 1946 and 1947.

The only definite record of the spawning of *N. macropterus* is given by Schaefer and Marr (p. 187). They demonstrate that yellowfin tuna spawn off the coast of Central America, at least from January into April; possibly into June. Kishinouye (1923: 448) states that "Some specimens examined in autumn at Kyushyu are said to have contained large ovaries." Herre (1940: 213) surmises that "extensive breeding grounds for yellowfin and oceanic bonito [=oceanic skipjack] exist in the Sea of Celebes and in that great section of the Pacific which lies east of Mindanao and north of New Guinea * * *." Lütken (1880) records a specimen of *Orcynnus germo* taken at 17° N., 115°40′ E. This may have been a young *Neothunnus macropterus*.

It seems not unlikely that more extensive studies over the entire ranges of the oceanic skipjack and the yellowfin tuna will reveal additional spawning areas. It is certain that extensive surveys will be necessary if the spawning habits of these fishes are to be understood.

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UNITED STATES DEPARTMENT OF THE INTERIOR, J. A. KRUG, Secretary
FISH AND WILDLIFE SERVICE, ALBERT M. DAY, Director

AGE AND GROWTH OF IMMATURE ROSEFISH (*SEBASTES MARINUS*) IN THE GULF OF MAINE AND OFF WESTERN NOVA SCOTIA

BY ALFRED PERLMUTTER AND GEORGE M. CLARKE

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AGE AND GROWTH OF IMMATURE ROSEFISH (*SEBASTES MARINUS*) IN THE GULF OF MAINE AND OFF WESTERN NOVA SCOTIA

The rosefish (*Sebastes marinus*) [1] is abundant on the fishing banks of the Gulf of Maine and Nova Scotia in depths ranging from 50 to 120 fathoms. Until 1935, rosefish were marketable only in limited quantities, and the yearly landings were well under 7,000,000 pounds. Technological advances in handling fish, particularly filleting, quick-freezing, and the perfection of an automatic scaling machine, in addition to the development of markets in Midwestern States, stimulated a rapid increase in the rosefish fishery to an average yearly catch of more than 100,000,000 pounds. The catch reached a peak in 1946 of 178,000,000 pounds. As a result of the growing importance of the fishery, the Fish and Wildlife Service began a study of the rosefish in the fall of 1942. This report summarizes one phase of the investigation; namely, the age and growth of immature rosefish in the Gulf of Maine and off the Browns Bank area of western Nova Scotia.

PREPARATION AND STUDY OF MATERIALS

STRUCTURES EXAMINED

From a preliminary examination of the bony structure of the rosefish it was found that the opercular bones, otoliths, and scales showed series of sculpturings, which, on the basis of previous age studies on other species of fish, were suggestive of year marks. Both the opercular bone and the otolith proved difficult to use in age analysis. In the opercular bone, the markings on some specimens were indistinct or were marred by a cavernous development near the base of the bone (fig. 1). The otoliths appeared more promising for determining the age of the rosefish. Freshly recovered otoliths or dried specimens cleared slightly in oil of cloves, oil of wintergreen, or glycerine, showed dark and light bands, as did cross sections of dry otoliths (figs. 2 and 3). Otoliths from the larger fish had a greater number of bands, but the individual rings were close together and less distinct. Because of the difficulty in collecting and preparing otoliths, and in distinguishing bands in the larger fish, together with the fact that only age data and no growth data could be obtained from otoliths, the study of them was discontinued. Attention was focused on the scales as a method of determining age and growth in rosefish.

Rosefish scales are oblong and strongly ctenoid on their outer edge, the number of rows of cteni being

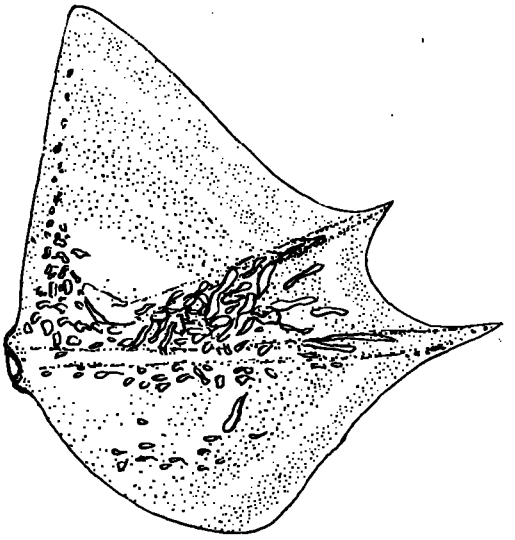

FIGURE 1.—Opercular bone showing growth bands. From a female rosefish 160 mm. long taken in the Gulf of Maine, January 1945. Enlarged 4 times.

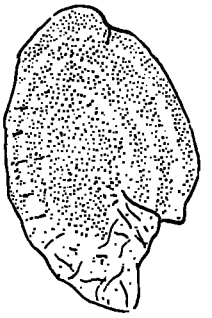

FIGURE 2.—Otolith showing growth bands. From a male rosefish 144 mm. long taken in the Gulf of Maine, November 1942. Enlarged 6 times.

[1] *Sebastes marinus* in American waters does not grow so large as its counterpart in European waters. The largest fish we have recorded in the Gulf of Maine was 48 cm. from the tip of the snout to the fork of the tail. Preliminary taxonomic comparison of recently collected data on the American fish with published data on the European fish indicates extensive variations of the genus throughout its range and the need for a complete taxonomic study.

greater on the scales of larger fish. Radii extend from the focus to the anterior margin of the scale and are more numerous in the larger than in the smaller fish. The circuli are distributed in bands of different spacings, and a band of wide-spaced circuli is generally followed by a band of narrow-spaced circuli.

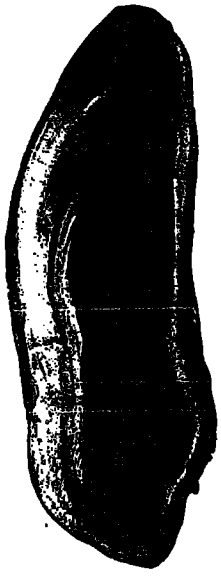

FIGURE 3.—Cross section of an otolith showing growth bands. From a female rosefish 70 mm. long taken in the Gulf of Maine, August 1943. Enlarged 30 times.

AREA OF FISH FROM WHICH SCALE SAMPLES WERE TAKEN

To determine the region on the body of the rosefish from which scales should be collected, the body was arbitrarily divided into 16 areas (fig. 4). Scales were taken from the midpoint of each of these areas and compared as to relative size, regularity, and circulus count. Four fish were examined in this manner. It was found that areas 11 and 13, the region covered by the tip of the pectoral fin and immediately posterior to it and adjacent to the lateral line, had the largest and most uniformly shaped scales with the highest circulus count (table 1). The relatively larger and more uniformly shaped scales from the "pectoral patch" were easier to mount and measure than scales from other parts of the body. Also, since scales from the "pectoral patch" area have the highest circulus count, it is most likely that they show maximum growth from the beginning of scale formation. All scale samples in the present study were taken from the "pectoral patch."

COLLECTION OF SCALE DATA

Scale collections were obtained from random lots of fish taken from individual trips of rosefish draggers. In each case, the boat captain was interviewed and

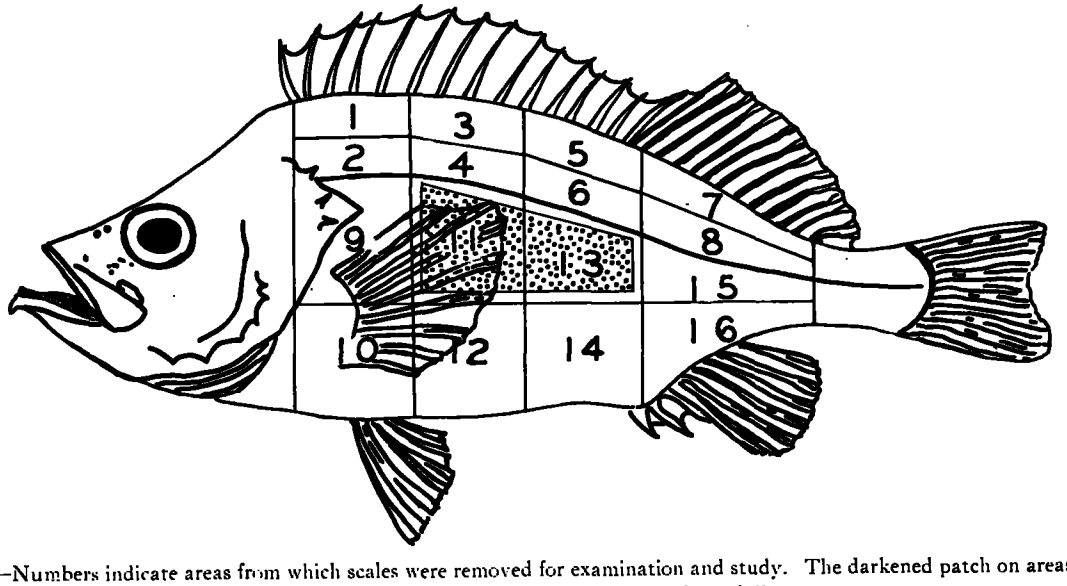

FIGURE 4.—Numbers indicate areas from which scales were removed for examination and study. The darkened patch on areas 11 and 13 is referred to in the text as the "pectoral patch."

TABLE 1.—*Circulus counts and anterior radii of rosefish scales from various body areas*

Circulus count					Anterior radius [1]				
Area	Specimen				Area	Specimen			
	1 [2]	2 [3]	3 [4]	4 [5]		1 [2]	2 [3]	3 [4]	4 [5]
1	80	56	78	143	1	118	77	122	210
2	108	76	129	164	2	205	110	239	261
3	84	82	84	139	3	142	113	132	197
4	94	98	105	208	4	149	166	195	383
5	97	88	94	164	5	166	118	148	246
6	105	113	102	195	6	207	180	192	351
7	88	77	89	173	7	149	116	140	262
8	101	95	143	191	8	196	139	270	340
9	98	114	129	223	9	264	198	267	455
10	105	106	112	228	10	241	200	160	427
11	125	120	146	250	11	282	230	314	468
12	106	106	123	231	12	227	178	242	461
13	117	125	144	253	13	261	220	297	509
14	112	108	138	237	14	227	195	266	438
15	111	115	142	244	15	230	217	286	445
16	110	110	122	196	16	225	173	220	353

[1] In millimerers, magnified 100 times.
[2] Male, 174 mm., Jeffreys Ledge, January 1943.
[3] Male, 154 mm., Jeffreys Ledge, January 1945.
[4] Female, 198 mm., Cashes, October 1943.
[5] Female, 304 mm., Cashes, October 1943.

reported fishing in only one biological area.[2] Only these "pure" trips were sampled in order to obtain homogeneous data from each area. The length of the fish was measured to the nearest millimeter by means of a measuring board.[3] These samples have been continuously collected since August 1942. Early in 1943, it was noticed that random sampling of the commercial catch resulted in few samples of scales from fish under 200 mm. in length. To obtain more adequate sampling of the fish in this size category, scale collections were taken from as many fish under 200 mm. as could be procured.

PREPARATION AND METHOD OF EXAMINING SCALE SAMPLES

Scales were mounted in corn syrup, or glycerine–gelatin, or dry, on glass slides, or were impressed on celluloid, depending on the size of the scale. Clearest mounts were obtained of the smaller scales, either dry, or after alizarin staining, in the liquid media. The larger scales were more easily handled as celluloid impressions. Each slide was given a code number. Data on size, sex, and locality were omitted from the label to prevent their influencing the investigators in determining the age readings.

[2] From a study of the degree of infestation of rosefish with the copepod parasite (*Sphyrion lumpi*) and information on the life history of the parasite, plus determination of centers of fishing concentration and the size composition of the catch at these places, the rosefish stock was subdivided into population units, but enclosed in various biological areas as follows: Mount Desert-Matinicus; Monhegan-Jeffreys-Platts: East of Gloucester-Highlands; Channel: Cigar Ridge-Cashes; and Browns Bank (fig. 5).

[3] Unless otherwise specified, all measurements of rosefish are from the tip of the snout to the fork of the tail.

All scales were read using a modification of the scale projector described by Van Oosten, Deason, and Jobes (1934). The machine was calibrated to produce an image 99.6 to 100.6 times the size of the object projected. Scale measurements used in the present analysis were based on an average magnification of 100 times. The projected image of the scale was measured along the median radius from the center of the focus to each annulus and to the anterior margin of the scale by marking off these distances on a strip of cardboard and then measuring them with a millimeter rule.

EXAMINATION OF SCALE MATERIAL

On the basis of scale studies on other species of fishes (Van Oosten 1929; Graham 1929), it is to be expected that the circulus bands present on rosefish scales represent periods of seasonal growth, a band of wide-spaced circuli being presumably the fast growth during summer, and a band of narrow-spaced circuli the slow growth in winter. Exploratory examination of the scales from all sizes of fish showed that the summer and winter bands were broad and could be most readily distinguished in fish less than approximately 235 mm. in length, but were narrow and difficult to determine with certainty for larger fish.

It was not possible to undertake a study of the age and growth of all sizes of rosefish because of limitations in facilities. Therefore, our study was confined to fish under 235 mm. in length. Size-at-maturity studies showed fish in this size category to be mainly

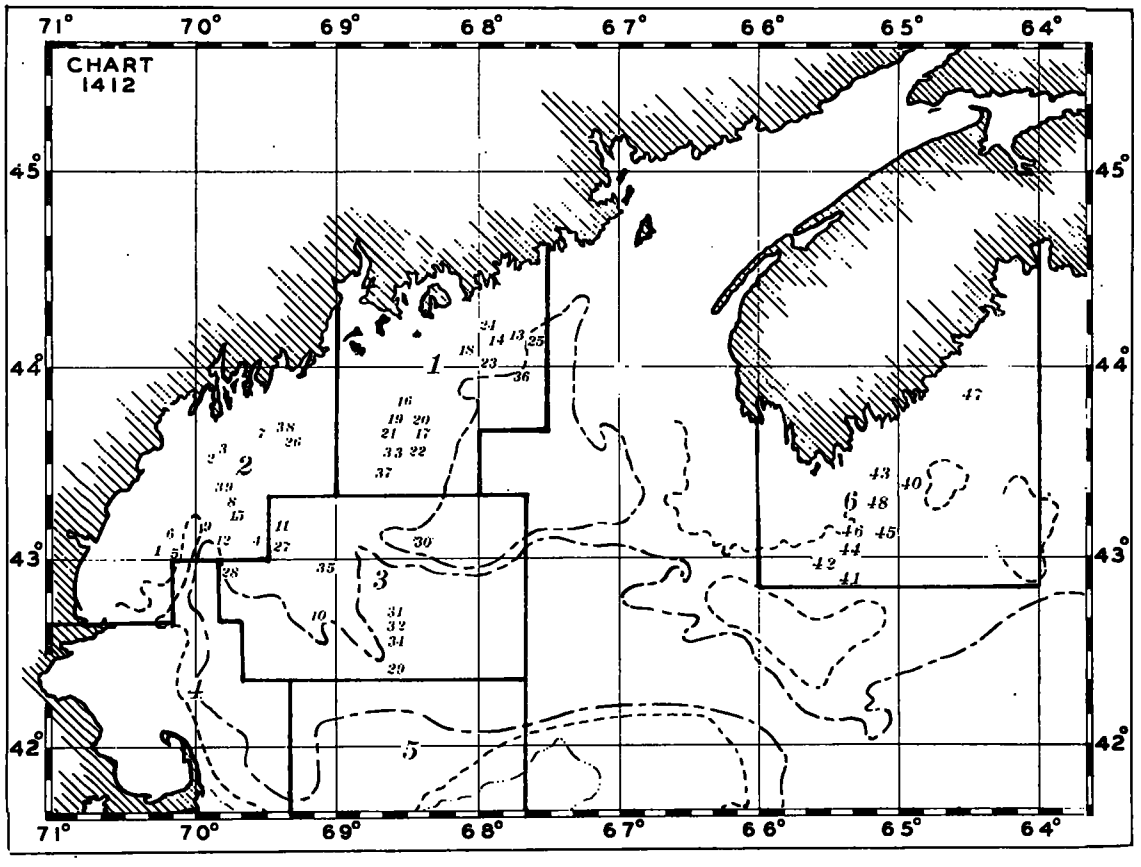

FIGURE 5.—Fishing concentration areas from which samples were obtained: area 1, Mount Desert-Matinicus; area 2, Monhegan-Jeffreys-Platts; area 3, Cigar Ridge-Cashes; area 6, Browns Bank area of western Nova Scotia (table 2). No collections of immature fish were obtained from area 4, east of Gloucester-Highlands, or from area 5, Channel, for the period studied.

TABLE 2.—*Collections used in the study of the age and growth of immature rosefish*

Collection No.	Year	Date landed	Area [1]	Number of fish	Collection No.	Year	Date landed	Area [1]	Number of fish
1	1942	Sept. 14	2	15	25	1944	June 17	1	5
2	1942	Oct. 16	2	5	26	1944	June 19	2	1
3	1942	Oct. 22	2	27	27	1944	July 1	3	6
4	1942	Nov. 3	2	34	28	1944	Aug. 21	3	1
5	1942	Dec. 15	2	5	29	1944	Aug. 26	3	1
6	1943	Feb. 11	2	37	30	1944	Aug. 28	3	1
7	1943	Mar. 20	2	6	31	1944	Oct. 10	3	1
8	1943	Mar. 29	2	3	32	1944	Oct. 13	3	4
9	1943	May 26	2	1	33	1944	Oct. 26	1	11
10	1943	May 28	3	9	34	1944	Oct. 27	3	3
11	1943	June 14	3	21	35	1944	Nov. 14	3	2
12	1943	June 15	2	1	36	1944	Nov. 22	1	1
13	1943	July 30	1	6	37	1944	Dec. 4	1	7
14	1943	Aug. 6	1	2	38	1944	Dec. 5	2	17
15	1943	Aug. 13	2	21	39	1944	Dec. 16	2	4
16	1943	Aug. 13	1	9	40	1942	Dec. 11	6	20
17	1943	Aug. 15	1	24	41	1943	Mar. 17	6	3
18	1943	Aug. 16	1	43	42	1943	Apr. 9	6	18
19	1942	Oct. 9	1	17	43	1943	June 4	6	11
20	1942	Oct. 29	1	8	44	1943	June 7	6	10
21	1942	Nov. 12	1	9	45	1943	June 8	6	2
22	1942	Nov. 20	1	8	46	1943	June 14	6	34
23	1942	Nov. 9	1	1	47	1943	Aug. 17	6	4
24	1942	Dec. 10	1	29	48	1943	Dec. 23	6	9

[1] Area 1 is the Mount Desert-Matinicus region; area 2, the Monhegan-Jeffreys-Platts region; area 3, the Cashes region; area 6, the Browns Bank region. See fig. 5 for a demarcation of these regions and the location of each collection point.

immature. For example, in 1943 and 1944 in the Gulf of Maine, 92 percent of the males and 99 percent of the females less than 235 mm. in length were immature, while in the Browns Bank area, 88 percent of the males and 98 percent of the females under 235 mm. were immature. The relatively few mature fish below 235 mm. were mostly in the size range from 225 to 234 mm., as shown in figure 6.

Scale samples obtained from random lots of the catch of the rosefish fleet included comparatively few from fish below 235 mm. in length, especially from those under 200 mm. To obtain a large amount of scale data for fish under 200 mm., scales were taken from as many fish in this size category as possible. Despite inclusion of the selected scale samples from the smaller fish, the total number of scale samples for fish under 235 mm. that could be procured from the commercial catch was relatively small. In the Gulf of Maine region, 158 scale samples were collected in 1942, 183 in 1943, and 65 in 1944, and these could only be obtained from fish in areas 1, 2, and 3, the Mount Desert-Matinicus, Monhegan-Jeffreys-Platts, and Cigar Ridge-Cashes areas, respectively. In the Browns Bank area off western Nova Scotia, 20 scale samples were collected in 1942 and 91 in 1943 (tables 2 and 3, and fig. 5).

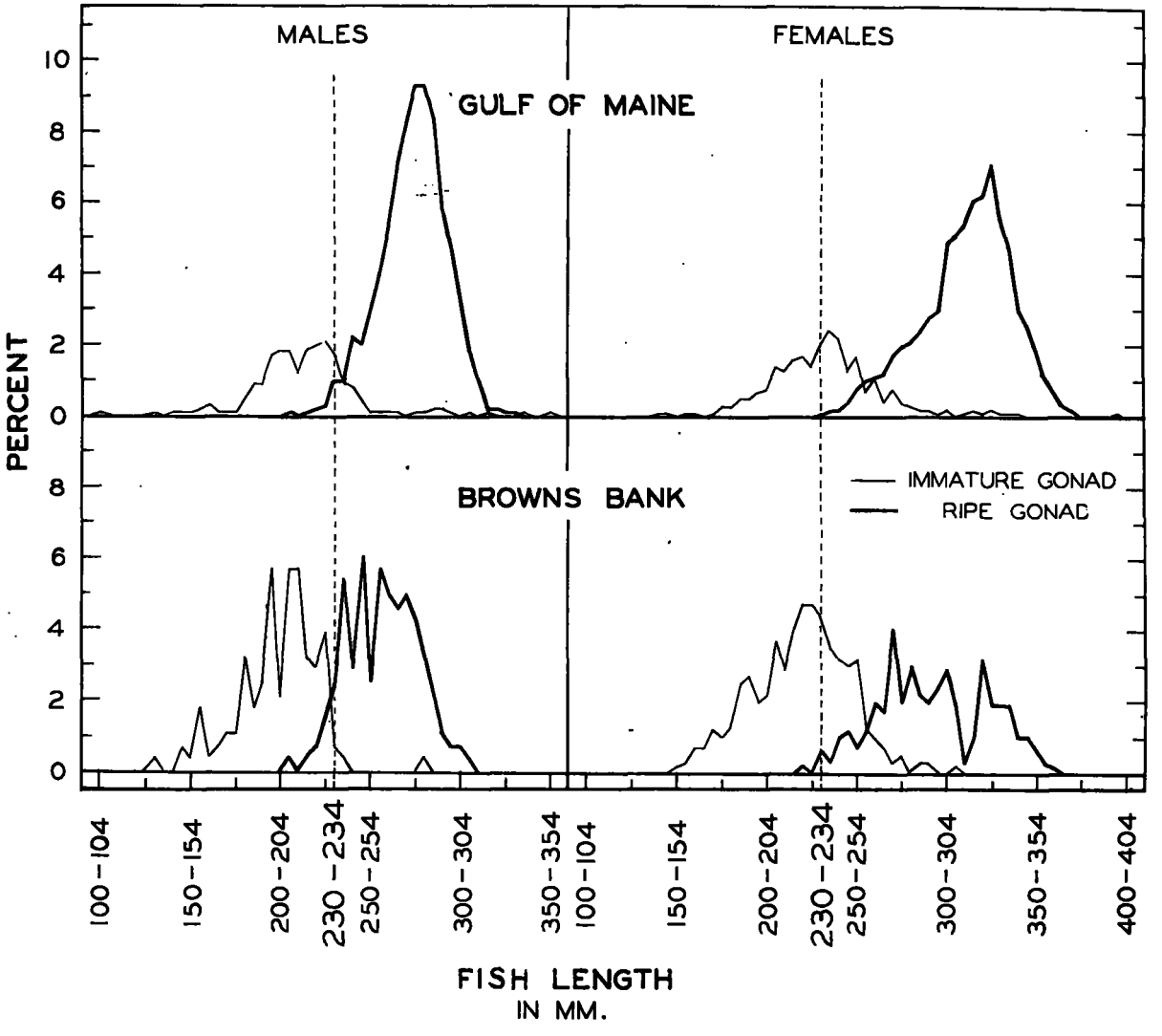

FIGURE 6.—Length-frequency distributions of immature fish by sex for the Gulf of Maine and the Browns Bank area. Gulf of Maine data: females examined in 1943 and 1944, 3,372; males examined in 1944, 1,644. Browns Bank data: females examined in 1943 and 1944, 591; males examined in 1944, 280.

TABLE 3.—*Length-frequency distribution of each collection of immature rosefish taken in the Gulf of Maine from September 1942 through December 1944 and in the Browns Bank area of western Nova Scotia December 1942 through December 1943*

Fish length in millimeters	Collection No.[1] 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
45–49																								
50–54																								
55–59																								
60–64																								
65–69																								
70–74															1									
75–79																	1							
80–84													1		1		2							
85–89													2		[2]1		2							
90–94				1									1			1	2					1		
95–99													2		4	2	1	2						
100–104																2	4	1						
105–109				1							1				4	1	3	2						
110–114			1	1											3	1	3	7				1		
115–119			1				1								1	1		6						
120–124			1	2		1											2	5						1
125–129			2	1		1									1			[3]3						1
130–134			1	1											1		1	[3]6				2		
135–139			1								1							2						2
140–144			1	4		3										[2]1	1	4	1					1
145–149	1		1	4		3									2		1	2						2
150–154			6	2											1		1	1	1		1	1		1
155–159			5	5	1	6									1			1						1
160–164	1				1	1	1				3							1						3
165–169	1		1	1	2	2					4			1					1	1				
170–174	5					7					2										1			3
175–179	2			2	1	4		1			1			1										4
180–184	2		1	1		1					6													
185–189	1		1	2		6			1										2		2			1
190–194	2			1		2	1			1	3								1	1		2		1
195–199				2				1																2
200–204		[2]1	3	2						3											1			1
205–209			1							1									1	1				1
210–214										2									1	1	2			3
215–219		2		1															3	2				
220–224							2	1				1							3	1				
225–229		2					1			1									1					1
230–234										1									2	1	2	1	1	
Total number of fish	15	5	27	34	5	37	6	3	1	9	21	1	6	2	21	·	24	43	17	8	9	8	1	29

Fish length in millimeters	Collection No.[1] 25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
45–49			1																					
50–54																								
55–59																								
60–64			1																					
65–69																								
70–74																								
75–79										1														
80–84			1																					
85–89			1							1														
90–94			1																					
95–99	2	1	1									1												
100–104						1																		
105–109					1				1	1										1				
110–114							1						1											
115–119	3							1							1	1								
120–124																[3]3								
125–129														1		1								
130–134									1						3	1						1		
135–139								1	2							2								
140–144								1	1					1		1								
145–149								1	2					3		2								
150–154									2							5					1	1		
155–159									1					2		2		1	1			1		1
160–164									1				1	1		2						3		
165–169				1							1		2	2				1	1			1		
170–174											1		2	6								1		
175–179													1	1					1			5		
180–184																						5		
185–189																		1	1	1		[4]7	1	
190–194																		2				[3]4		[2]1
195–199																			1			3		
200–204																			1			2		2
205–209																		1	3					
210–214																	1	5	[2]1					
215–219																		1		1				1
220–224																		2					1	1
225–229																	1	2		5				
230–234																	1	2	1	[3]2	1		2	3
Total number of fish	5	1	6	1	1	1	1	4	11	3	2	1	7	17	4	20	3	18	11	10	2	34	4	9

[1] Information on date of collection and area is shown in table 2.
[2] Not read. All scales on the slide either showed regenerated centers or the impressions were indistinct.
[3] Scales from 1 fish could not be read either because all scales showed regenerated centers or the impressions were indistinct.
[4] Scales from 2 fish could not be read either because all scales showed regenerated centers or the impressions were indistinct.

Fishing selectivity largely accounts for the small numbers of fish less than 235 mm. found in the commercial catch and is due to the fact that rosefish less than 8 inches long (200 mm.) are not marketable at Gloucester. Consequently, the fishermen avoid concentrations of small fish. In most instances, this is not difficult, as there appears to be a definite segregation of the smaller or immature fish, from the larger or mature fish. Under normal conditions when small fish are inadvertently captured, they are culled and thrown overboard at sea. It is apparent, then, that large numbers of scale samples from small fish can best be procured by means of an experimental vessel fishing in the nursery areas. Pending such collection, it was deemed advisable to study the available data to obtain preliminary information on the age and growth of the rosefish.

PROCEDURE FOR DETERMINING AGE AND GROWTH FROM SCALES

SIGNIFICANCE OF CIRCULUS BANDS ON ROSEFISH SCALES

On the basis of scale studies on other species of fishes, it is to be expected that the circulus bands present on the rosefish scale represent periods of seasonal growth. To test this hypothesis a study was made of the scales of 229 fish less than 225 mm. in length taken in the Gulf of Maine in the period from April 1942 through June 1943. The part of the scale from the last circulus in the last band of narrow-spaced circuli to the edge of the scale was designated the "terminal-zone." It was observed that all specimens had only wide-spaced circuli in this zone in April through May 1942. By November 1942, the marginal circuli of the zone were closer together in some specimens and, in February 1943, in most specimens. By April 1943, all the circuli in the terminal-zone were once again widely separated.[4] Furthermore, the circulus count and size of the terminal-zone increased from April–May 1942 until February–March 1943, when there was an abrupt decrease in these characters in a few of the fish, and by April 1943, in all of the fish (fig. 7, table 4). The sudden decrease in the circulus count and in the size of the terminal-zone in April 1943 can be explained by the completion of the band of narrow-spaced circuli ending another year's growth and the inception of a new band of wide-spaced circuli starting the next year's growth.

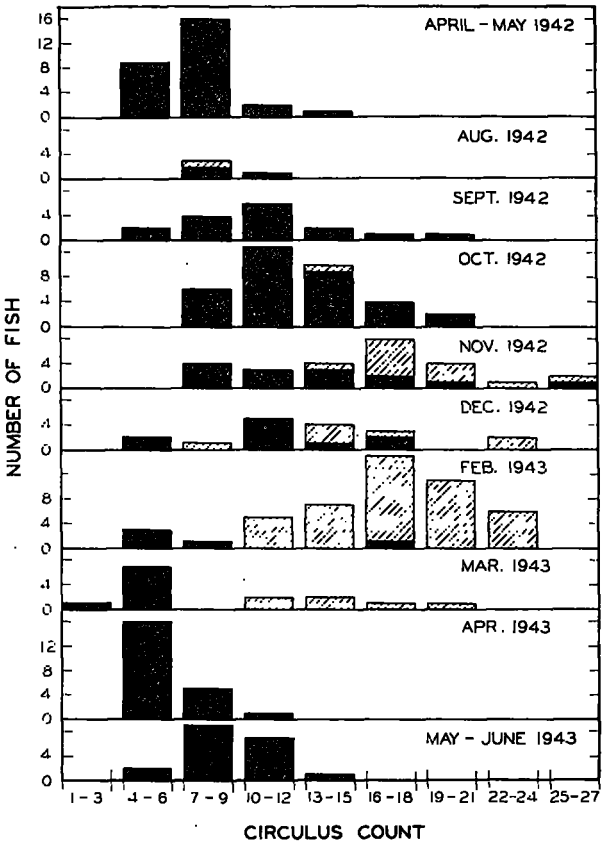

FIGURE 7.—Circulus counts from the last band of narrow-spaced circuli to the edge of the scale (terminal-zone) for scales collected from rosefish less than 225 mm. in length taken in the Gulf of Maine from April 1942 through June 1943. The solid bars indicate wide-spaced circuli, and the diagonal lines narrow-spaced circuli at the edge of the terminal-zone.

From these data it can be seen that the narrow-spaced and wide-spaced circulus bands on the rosefish scale, as on the scales of other fishes, denote seasonal growth intervals. During April through October, growth is most rapid and a band of wide-spaced circuli is formed. From November through March, growth slows down and a band of narrow-spaced circuli results. The narrow-spaced band of circuli is considered the annular band or annulus. In the annular band, the circuli do not continue posteriorly along the lateral margins of the scale as they do in the band of wide-spaced circuli, but instead, most of them end abruptly or merge at the lateral margin of the scale forming a characteristic broken pattern. Examples of scales with varying

[4] Bands of wide-spaced and narrow-spaced circuli are readily distinguishable from each other upon examination. Nevertheless, a more objective method of differentiating between wide- and narrow-spaced circuli was attempted by caliper measurements of circuli widths. Physical limitations in our apparatus plus certain inherent limitations in the material caused us to discontinue this technique.

TABLE 4.—*Time of formation of narrow and wide bands in rosefish less than 225 mm. in fish length*

Number of circuli [1]	Number of fish																			
	April–May 1942		August 1942		September 1942		October 1942		November 1942		December 1942		February 1943		March 1943		April 1943		May–June 1943	
	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]
1–3															1					
4–6	9				2						2		3		7		16		2	
7–9	16		2	1	4		6		4			1	1				5		9	
10–12	2		1		6		13		3		5			5		2	1		7	
13–15	1				2		9	1	3	1	1	3		7		2			1	
16–18					1		4		2	6	2	1	1	14		1				
19–21					1		2		1	3				11		1				
22–24										1		2		6						
25–27									1	1										
28–30																				
Total	28		3	1	16		34	1	14	12	10	7	5	43	8	6	22		19	

Zone growth [4]	Number of fish																			
	April–May 1942		August 1942		September 1942		October 1942		November 1942		December 1942		February 1943		March 1943		April 1943		May–June 1943	
	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]	Wide [2]	Narrow [3]
0–4																				
5–9	1			1	1						1	1			2		3			
10–14	6				1		1		1		1		3		6		10			
15–19	14		2		1		4		2				1				6		4	
20–24	4				6		5		4					2		2	2		6	
25–29			1		1		10		2	1	2	1		3		1			7	
30–34	2				3		7	1		1	3	1		6		2	1		2	
35–39	1						3		1	1	1	2		12						
40–44					2		3		2	5			1	9		1				
45–49					1					2	2			2						
50–54							1							5						
55–59									2	2		1		1						
60–64												1		2						
65–69														1						
70–74																				
Total	28		3	1	16		34	1	14	12	10	7	5	43	8	6	22		19	

[1] Number of circuli from the edge of the last band of narrow-spaced circuli to the scale margin.
[2] Wide phase; wide-spaced circuli only.
[3] Narrow phase; wide-spaced circuli followed by narrow-spaced circuli at the scale margin.
[4] The median radial distance in millimeters from the edge of the last band of narrow-spaced circuli to the scale margin, magnified 100 times.

numbers of annuli are shown in figures 8 through 15. Figures 8 and 9 are scales from fish 30 and 50 mm. in length, respectively, which were captured in October. They show no annuli but consist entirely of wide-spaced circuli. Figure 10, a scale from a fish 59 mm. in length, has one annulus, and figures 11 through 15 contain two, three, four, six, and eight annuli, respectively.

AGE OF ROSEFISH AT TIME OF SCALE FORMATION

Although scale readings give the age of the rosefish from inception of the scale to the time of capture, they do not furnish any information on the extent of the period preceding initial scale formation. The rosefish is ovoviviparous, and from a study of the relative frequency of various developmental stages of the embryos contained in the ovaries of the fish throughout the spring and summer, it was found that the Gulf of Maine rosefish extrude the young from mid-May through early September, with the peak birth period in July. The size at birth is indicated by larvae taken from a 297-mm. fish caught in the Mount Desert-Matinicus area in August 1943. These larvae still retained the yolk sac but swam actively when placed in a container of salt water. A sample of the specimens ranged from 7.1 to 7.5 mm. in total length. Our findings on the rosefish in Gulf of Maine waters confirm those of Bigelow and Welsh (1925:308) and are also in agreement with those of Frost (1938:15) in Newfoundland waters, which suggest a similar rosefish birth period in both areas.

According to Bigelow and Welsh (1925:311, fig. 147) rosefish larvae 20 mm. in length do not have scales. Therefore, in order for newly born larvae

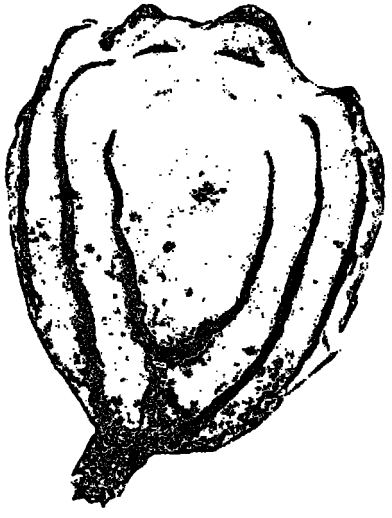

FIGURE 8.—Scale showing only four wide-spaced circuli, no annuli, from a fish 30 mm. long captured in the Cigar Ridge-Cashes area, October 1946.

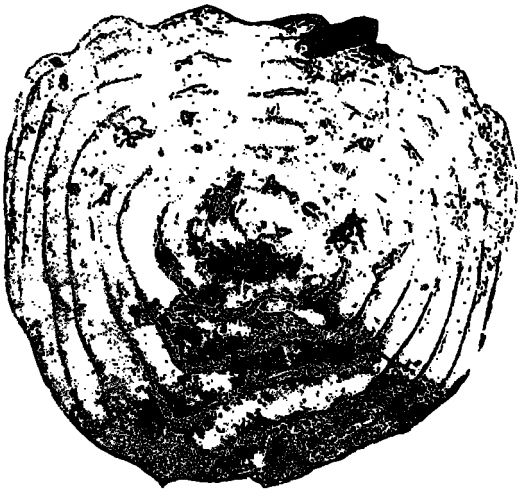

FIGURE 9.—Scale showing only eight wide-spaced circuli, no annuli, from a fish 50 mm. in length captured in the Mount Desert-Matinicus area, October 1944.

to show the first annular ring in April of the following year, they must grow longer than 20 mm. by the fall of the year in which they are born so that a series of wide-spaced circuli can be formed. Information on the growth of larval rosefish on the Gulf of Maine or Nova Scotian fishing grounds is not available but is indicated by data obtained from Newfoundland grounds. During cruises of the research vessel *Cape Agulhas* in Newfoundland waters in the spring and summer of 1932 to 1935, a large series of rosefish larvae were taken, chiefly by plankton nets.[5] The lengths of these larvae are summarized by months and years of collection in table 5.

An examination of these data shows that for all years combined the mode of the length frequency was 7 mm. in May, 8 mm. in June, 9 mm. in July and August, and 10 mm. in September, indicating

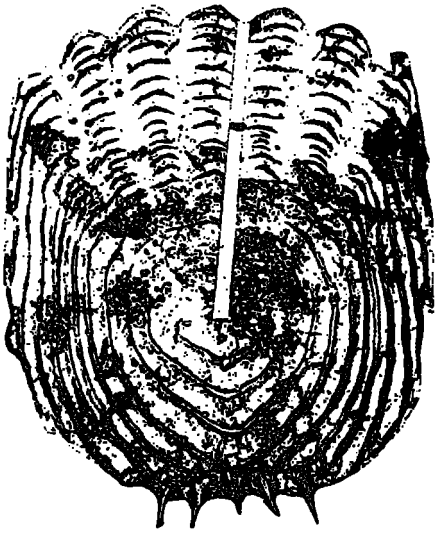

FIGURE 10.—Scale showing one annulus and initial formation of the wide-spaced circuli band of the second year band. From 59-mm. male captured in the Monhegan-Jeffreys-Platts area, April 1946.

FIGURE 11.—Scale showing two annuli and initial formation of the wide-spaced circuli band of the third year band. From a female 102 mm. long, captured in the Monhegan-Jeffreys-Platts area, June 1946.

[5] The general area of capture for these fish is shown in a paper by Frost (1938). A copy of the original length data was made available by the Newfoundland Department of Natural Resources through the courtesy of the director Dr. Wilfred Templeman.

extremely slow growth. In May at the beginning of the birth period, two fish, 20 and 21 mm. in length, were also taken. According to the growth data, these fish could not have reached so large a size if they had been born in April or May of the year in which they were captured. They must have been born in the previous year because fish of this size do not have scales.

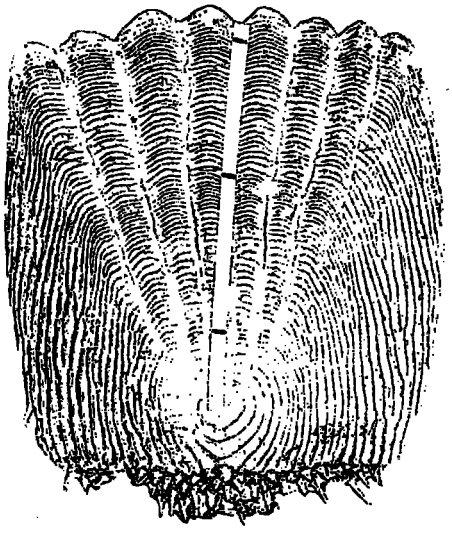

FIGURE 12.—Scale showing three annuli. From a male, 122 mm. long, captured east of Gloucester-Highlands area, March 1946.

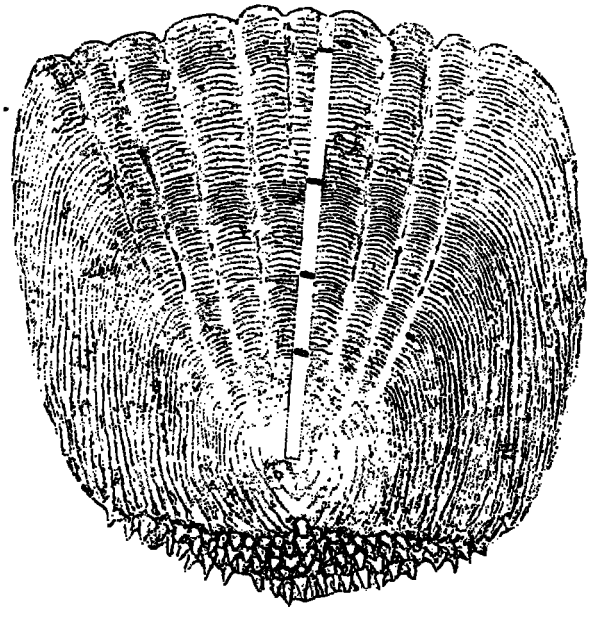

FIGURE 13.—Scale showing four annuli. From a female, 144 mm. long, captured in the Monhegan-Jeffreys-Platts area, April 1946.

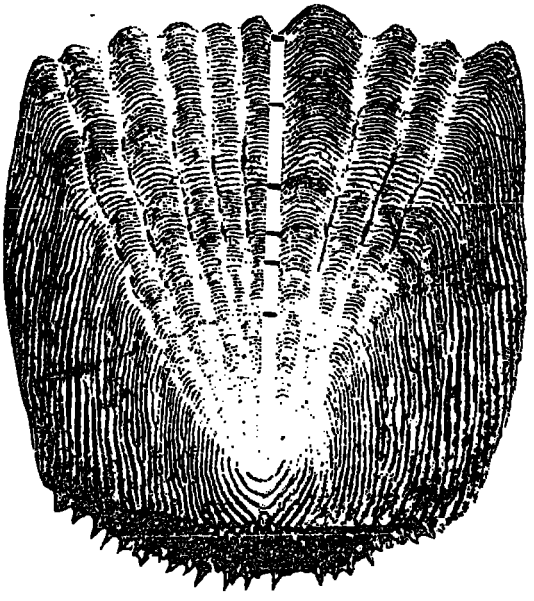

FIGURE 14.—Scale showing six annuli. From a male, 159 mm. long, captured in the Browns Bank area, May 1946.

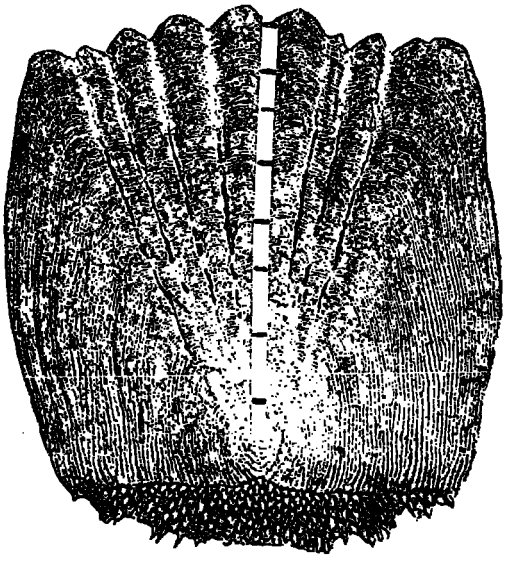

FIGURE 15.—Scale showing eight annuli. From a male, 234 mm. long, captured in the Monhegan-Jeffreys-Platts area, April 1946.

Rosefish, 37 to 55 mm. in total length, obtained in the Gulf of Maine in October of 1944 [6] and 1946 [7] show scales having a band of wide-spaced circuli and a few narrow-spaced circuli. The scales must have formed when the fish were more than 20 mm. and less than 37 mm. in length and, apparently, during the year in which the fish were captured. On the

[6] Five fish, 50–55 mm. long, taken in the Mount Desert-Matinicus area.

[7] Six fish, 37–51 mm. long, taken in the Cigar Ridge-Cashes area.

TABLE 5.—*Lengths of larval rosefish taken in Newfoundland waters* [1]

Larva length in millimeters	May	June				July			August					September				All years				
	1932	1932	1933	1934	1935	1933	1934	1935	1931	1932	1933	1934	1935	1931	1932	1933	1935	May	June	July	August	September
5	1	1						1										1	1	1		
6	7		11	1			1	1	16		1					1		7	12	2	17	1
7	23	3	28	21	2	1	15	5	33					1			1	23	54	21	33	2
8	5		75	34	23	16	20	4	27	2		1		1		1		5	132	40	30	2
9			20	16	3	24	6	12	53	1	3		2		1		1		39	42	59	2
10				5		4	1	6	41	1	2		3	1	2				5	11	47	3
11	1	1		1					10	1			1		1			1	2		12	1
12	1	1	1	1					1									1	3		1	
13				1					1			2							1		3	
14									1												1	
15												1	1								2	
16									1												1	
17																						
18																						
19									1												1	
20	1																	1				
21	1																	1				
22																						
23																						
24																						
25																						
26														1								1
27																						
28																						
29																						
30																						
31																						
32																						
33																						
34																						
35																						
36																						
37																	1					1
Total	40	6	135	80	28	45	43	29	185	5	6	4	7	4	4	2	3	40	249	117	207	13

[1] These fish were caught by the research vessel *Cape Agulhas*. The general area of capture is shown in a paper by Frost (1938).

basis of the foregoing information, these fish must have been born in 1943 and 1945, respectively. The scales began to form in 1944 and 1946, respectively, and by March 1945 and 1947, respectively, would show the first annular ring. Therefore, in the present age and growth study, the calendar year of birth of a rosefish is obtained by adding one additional year to the total number of annuli shown on the scale.

METHODS OF ANALYSIS

Two procedures were followed in estimating the lengths of rosefish at past ages from the spacing of the annuli. In both, a straight line was fitted to the logarithmic values for fish lengths plotted against scale radius. In the first use of this line the constant term in the logarithmic equation was employed in deriving the following formula by means of which lengths were computed directly from scale measurements.

$$Ln = C + \frac{Sn}{S}(L - C)$$

C—is the intercept value at the X axis of a straight line fitting the data.

L—the log of the length of the fish when caught.

Ln—the log of the computed length of the fish at the end of any year.

S—the log of the anterior scale radius of the fish when caught.

Sn—the log of the anterior scale radius to any annulus.

The second method follows the procedure used by Hile (1941) in the study of the age and growth of the rock bass (*Ambloplites rupestris*). Essentially, it involves the solution of the logarithmic equation to build up a table of theoretical scale lengths at different body lengths. Before the measurements for a particular scale can be used for reading the calculated length from the table, each must be adjusted according to the ratio of the theoretical to the actual scale size.

On theoretical grounds the two procedures can give identical results only if before application of the formula (first procedure) the scale measurements are adjusted to the theoretical values in the same manner as that followed by Hile. It is easy to demonstrate that strictly accurate results are obtained from

TABLE 6.—*Comparison of average calculated fish-length values, in millimeters, at each annulus*

[Material collected in Monhegan-Jeffreys-Platts area, October–December 1942]

Calculated from fish born in—	Annulus 1		2		3		4		5		6		7		8		9		Number of fish
	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	
1932	47	47	70	70	98	98	111	112	132	132	149	149	167	166	191	191	204	203	2
1933	49	49	72	72	89	88	120	120	144	144	166	166	184	184	200	199	------	------	2
1934	44	44	73	72	95	95	119	118	139	139	157	157	175	175	------	------	------	------	9
1935	50	50	74	74	97	97	118	118	137	136	158	158	------	------	------	------	------	------	19
1936	46	46	79	79	107	107	131	131	154	154	------	------	------	------	------	------	------	------	9
1937	51	51	78	78	111	111	131	131	------	------	------	------	------	------	------	------	------	------	12
1938	50	50	73	73	105	104	------	------	------	------	------	------	------	------	------	------	------	------	11
1939	50	50	91	91	------	------	------	------	------	------	------	------	------	------	------	------	------	------	5
1940	57	57	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	1
Weighted mean	49	49	76	76	102	102	123	123	141	141	158	158	175	175	196	193	204	203	--------
Number of fish	70		69		64		53		41		32		13		4		2		--------

[1] Method 1.—Calculations were based on a straight line fitted to the logarithmic values for fish lengths and scale radii obtained from material collected from October–December 1942 in the Monhegan-Jeffreys-Platts area; collections 2–5, 71 fish. Scales for 1 fish could not be read because no good scales were on the slide.
[2] Method 2.—Calculations were based on a curve fitted to the arithmetical values for fish lengths and scale radii for the same material analyzed by method 1.

TABLE 7.—*Comparison of average calculated fish-length values, in millimeters, at each annulus*

[Material collected in Mount Desert-Matinicus area, July–September 1943]

Calculated from fish born in—	Annulus 1		2		3		4		5		6		7		Number of fish
	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	A [1]	B [2]	
1935	50	49	60	60	94	93	116	116	131	131	145	145	159	159	1
1936	53	54	74	74	90	90	104	104	129	129	144	144	------	------	5
1937	55	54	76	76	97	96	113	113	133	133	------	------	------	------	9
1938	54	54	73	73	92	92	110	110	------	------	------	------	------	------	23
1939	58	58	77	77	96	96	------	------	------	------	------	------	------	------	14
1940	60	60	78	79	------	------	------	------	------	------	------	------	------	------	25
1941	67	67	------	------	------	------	------	------	------	------	------	------	------	------	4
Weighted mean	57	57	76	76	94	94	110	110	132	132	144	144	159	159	--------
Number of fish	81		77		52		38		15		6		1		--------

[1] Method 1.—Calculations were based on a straight line fitted to the logarithmic values for fish lengths and scale radii obtained from material collected from July–September 1943 in the Mount Desert-Matinicus area (collections 13, 14, 16, 17, 18; 84 fish). 3 fish could not be read because no good scales were on the slide.
[2] Method 2.—Calculations were based on a curve fitted to the arithmetical values for fish lengths and scale radii for the same material analyzed by method 1.

the formula only when the scale measured is of exactly the theoretical length. That the errors arising from deviations of the measured scales from the theoretical values have no important effect on the averages of calculated lengths for groups of fish is demonstrated, however, by the extremely close agreement between the results obtained independently by the two procedures (tables 6 and 7). The discrepencies were few and always no more than a millimeter. For practical purposes either procedure can be followed. The second is preferable, not only because it is easier to follow, but also because it gives accurate calculations for individual fish as well as for group averages.

VARIATIONS IN THE FISH LENGTH-SCALE RADIUS RELATIONSHIP

Since both methods of calculating from scales the size at a previous age employ the fish length-scale radius relationship, variations in this relationship from season to season or from one biological area to another would result in different values for estimated lengths. A comparison of the slope of the lines describing the fish-length and scale-length relationship at different seasons in various areas was attempted but discontinued because of the small amount of data available for many of these seasonal-area units. Instead, a more general approach was employed.

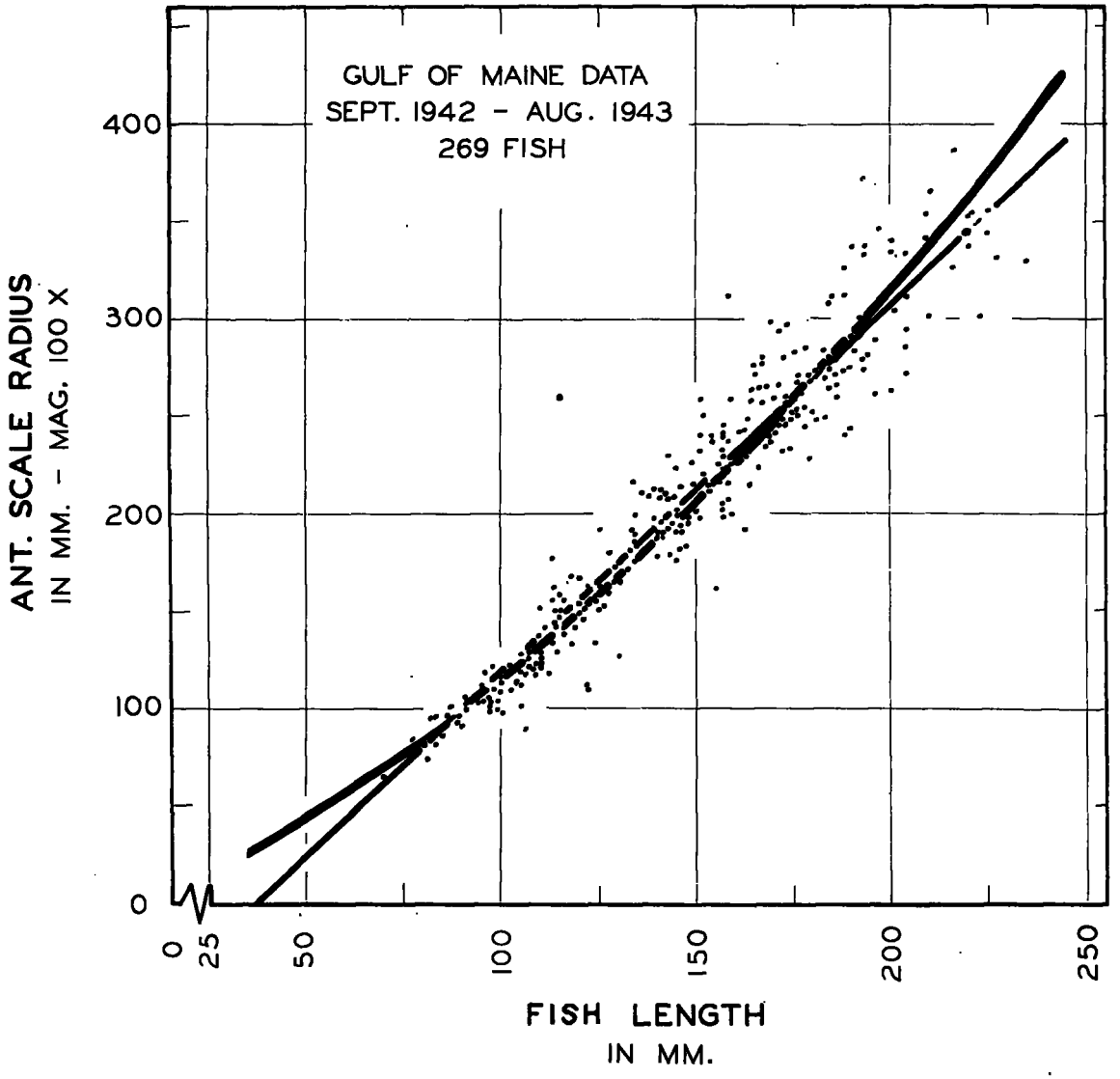

FIGURE 16.—Relationship in arithmetical terms of the anterior scale radius to the length of rosefish for 269 fish 235 mm. or less, taken in the Gulf of Maine from September 1942 through August 1943. Both the straight line and curve were calculated to fit the data. The formula for the straight line is $y = -68.84 + 1.88\,x$.

Examination of the individual collections made in the Gulf of Maine from September 1942 through December 1944 shows three series of collections containing a relatively large number of fish which fall into one biological area during a single calendar quarter; namely, a series in the Mount Desert-Matinicus area from October through December 1942,[8] in the same area from July through September 1943,[9] and in the Monhegan-Jeffreys-Platts area from October through December 1942.[10] The estimated length at each age was calculated independently for each of the three sets of data. The resulting values were then combined and the average calculated lengths at each age obtained (table 8, column A).

At the same time, the fish length-scale radius relationship was determined for all material collected in the Gulf of Maine from September 1942 through August 1943.[11] On the basis of this rela-

[8] Collections 19–24: 72 fish; table 2, fig. 5.
[9] Collections 13, 14, and 16–18: 84 fish; table 2, fig. 5.
[10] Collections 2–15: 71 fish; table 2, fig. 5.
[11] Collections 1–18: 269 fish; figures 16 and 17.

TABLE 8.—*Comparison of average calculated fish length values, in millimeters, at each annulus computed from lines fitted separately to length—scale data for various areas at various time intervals and from a single line fitted to length—scale data*

[Collections made in the Gulf of Maine from September 1942 through August 1943]

Calculated from fish born in—	Annulus																	
	1		2		3		4		5		6		7		8		9	
	A[1]	B[2]	A[1]	B[2]	A[1]	B[2]	A[1]	B[2]	A[1]	B[2]	A[1]	B[2]	A[1]	B[2]	A[1]	B[2]	A[1]	B[2]
1932	47	48	74	79	96	104	118	112	137	133	155	146	172	163	189	186	202	195
1933	49	52	76	75	98	98	122	120	141	141	163	158	182	174	201	192	------	218
1934	47	51	75	75	99	96	123	116	144	133	164	151	183	167	------	190	------	------
1935	49	55	73	77	98	99	119	120	139	137	161	157	159	174	------	162	------	------
1936	49	50	77	76	103	103	124	123	146	145	144	150	------	157	------	------	------	------
1937	53	52	78	78	104	104	124	125	133	138	------	149	------	------	------	------	------	------
1938	52	51	73	75	97	100	110	120	------	------	------	------	------	------	------	------	------	------
1939	56	52	80	76	96	96	------	124	------	------	------	------	------	------	------	------	------	------
1940	59	54	75	74	------	95	------	------	------	------	------	------	------	------	------	------	------	------
1941	67	58	------	81	------	------	------	------	------	------	------	------	------	------	------	------	------	------
1942	------	55	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
Weighted mean	52	52	75	76	99	99	120	121	141	139	161	154	180	169	196	189	202	218
Number of fish	222	308	218	297	186	251	158	203	116	139	89	90	51	38	23	12	10	3

[1] Straight lines were fitted independently to logarithmic values for fish lengths and scale radii obtained from material collected in the Mount Desert-Matinicus area from July-September 1943 (collections 13, 14, 16, 17, 18; 84 fish); in the same area from October–December 1942 (collections 19–24; 72 fish); in the Monhegan-Jeffreys-Platts area from October–December 1942 (collections 2–5; 71 fish). No good scales were available for 1 fish in collection 2, for 1 fish in collection 16, and for 2 fish in collection 18. The data collected in each area during each 3-month interval was analyzed by method 1 using the corresponding line.

[2] A curve was fitted to the values for fish lengths and scale radii obtained from material collected throughout the Gulf of Maine from September 1942 through August 1942 (collections 1–18; 269 fish). Data collected throughout the Gulf of Maine in 1942 (collections 1, 3, 4, 6; 113 fish) in 1943 (collections 10, 11, and 13–18; 131 fish), and in 1944 (collections 25–39; 65 fish) were analyzed by method 2 using this curve.

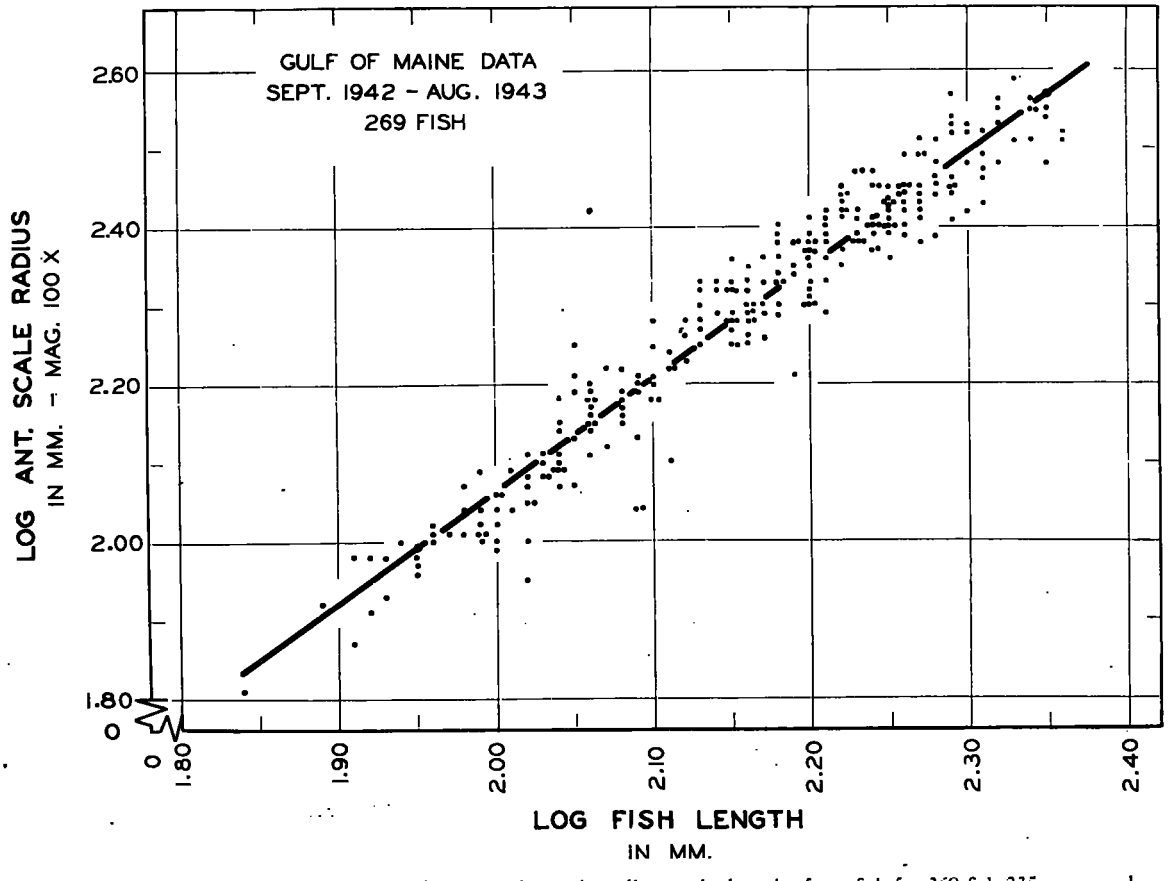

FIGURE 17.—Relationship in logarithmic terms of the anterior scale radius to the length of rosefish for 269 fish 235 mm. or less, taken in the Gulf of Maine from September 1942 through August 1943. The straight line was calculated to fit the data. Its formula is $\log y = -.831 + 1.447 \log x$.

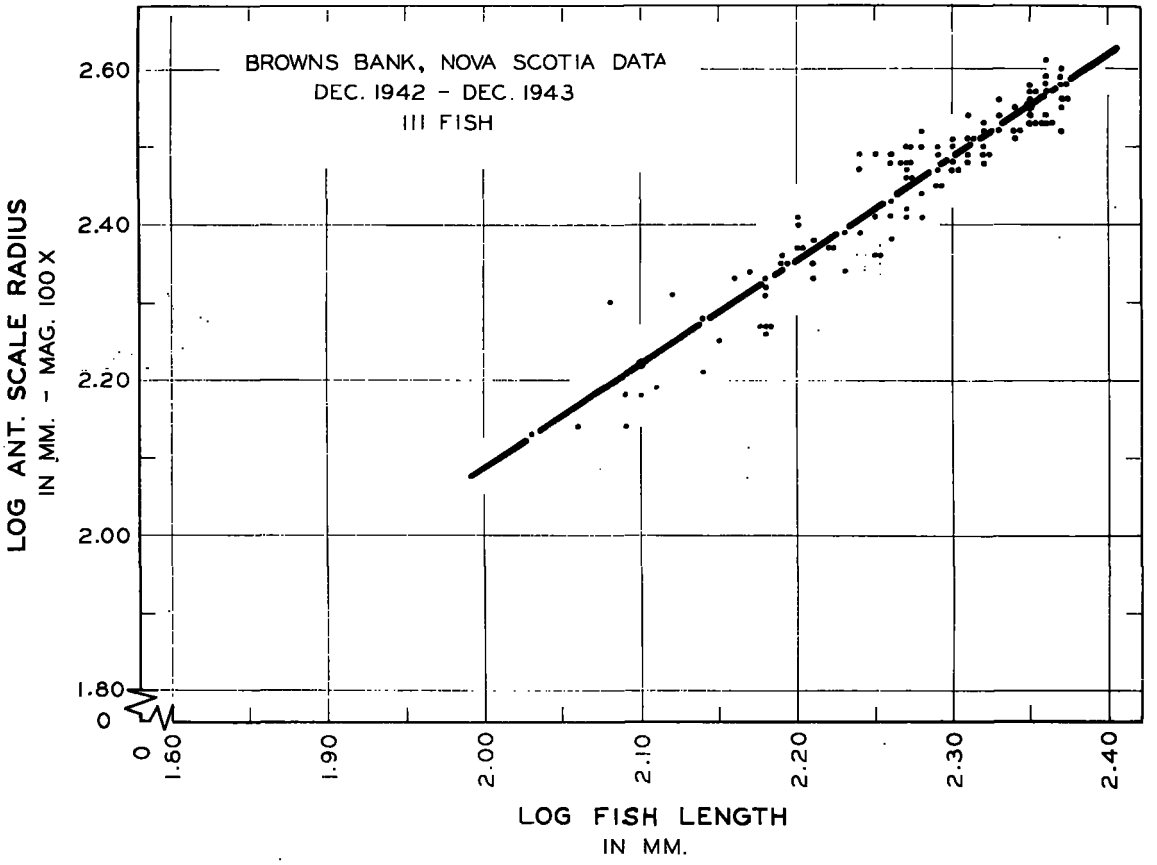

FIGURE 18.—Relationship of the anterior scale radius to the length of rosefish for 111 fish, 235 mm. or less, taken in the Browns Bank area of western Nova Scotia from December 1942 through December 1943. The straight line was calculated to fit the data. Its formula is $\log y = -.596 + 1.340 \log x$.

tionship, the estimated age at each annulus was calculated for data collected throughout the Gulf of Maine in 1942,[12] 1943,[13] and in 1944.[14] The average calculated lengths obtained are shown in table 8, column B.

The values for average calculated lengths at each annulus obtained from computations based on the individual sets of data and the total data are in close agreement. This would indicate that variation in fish length-scale radius relationship, both seasonal and from one biological area to another, does not greatly affect the accuracy of calculated length values. Therefore, the calculated length values for the combined data were accepted as the best available estimates of rosefish length at a given age. Similarly, the estimated age at each annulus was calculated from the fish length-scale radius relationship for all data collected from December 1942 through December 1943 in the Browns Bank area of western Nova Scotia (fig. 18).

[12] Collections 1, 3, 4, 6: 113 fish.
[13] Collections 10, 11, and 13–18: 131 fish.
[14] Collections 25–39: 65 fish.

RESULTS

CALCULATED LENGTHS AT EACH ANNULUS

The data collected in 1942, 1943, and 1944 were analyzed separately, and the calculated sizes obtained for the 3 years are summarized in table 9. The estimated average length of the fish at each annulus varies at random among the different year classes but the variation is remarkably small. The weighted mean estimated length at each annulus of all the year classes is as follows: annulus 1, 52 mm.; annulus 2, 76 mm.; annulus 3, 99 mm.; annulus 4, 121 mm.; annulus 5, 139 mm.; annulus 6, 154 mm.; annulus 7, 169 mm.; annulus 8, 189 mm.; and annulus 9, 218 mm. (table 10, fig. 19). The estimated average lengths of the rosefish at each annulus in the Browns Bank area of western Nova Scotia are similar to those obtained in the Gulf of

TABLE 9.—*Average calculated fish length, in millimeters, at each annulus* [1]

[Calculations [2] based on method 2]

Calculated from fish born in—	Annulus 1	2	3	4	5	6	7	8	9
1932 [3]	48	79	104	112	133	146	163	186	195
1933	52	75	98	120	141	158	174	192	218
1934	51	75	96	116	133	151	167	190	----
1935	55	77	99	120	137	157	174	162	----
1936	50	76	103	123	145	150	157	----	----
1937	52	78	104	125	138	149	----	----	----
1938	51	75	100	120	143	----	----	----	----
1939	52	76	96	124	----	----	----	----	----
1940	54	74	95	----	----	----	----	----	----
1941	58	81	----	----	----	----	----	----	----
1942	55	----	----	----	----	----	----	----	----
Weighted mean	52	76	99	121	139	154	169	189	218
Standard deviation	7.92	10.53	14.62	17.37	16.89	16.72	19.47	16.51	----
Number of fish	308	297	251	203	139	90	38	12	3

[1] Includes materials collected in the Gulf of Maine in 1942 (collections 1, 3, 4, 6; 113 fish), in 1943 (collections 10, 11, and 13–18; 131 fish), and in 1944 (collections 25–39; 65 fish). Data combined for the years 1942, 1943, and 1944.

[2] Data collected throughout the Gulf of Maine from September 1942 through August 1943 (collections 1–18; 269 fish) were used in deriving the curve employed in obtaining calculated lengths at each annulus by means of method 2.

[3] Only 1 fish was available, and it has not been included in the statistical calculations.

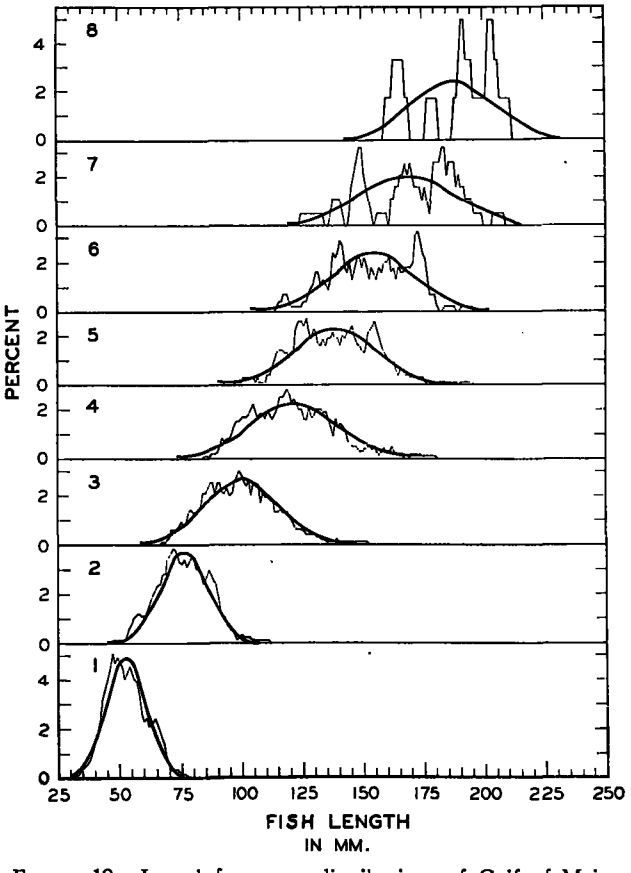

FIGURE 19.—Length-frequency distributions of Gulf of Maine rosefish at each annulus for annuli 1 through 8. Lightly lined irregular curves are the actual frequency distributions smoothed by a moving average of five. Heavily lined smooth curves are normal curves fitted to the actual frequency data.

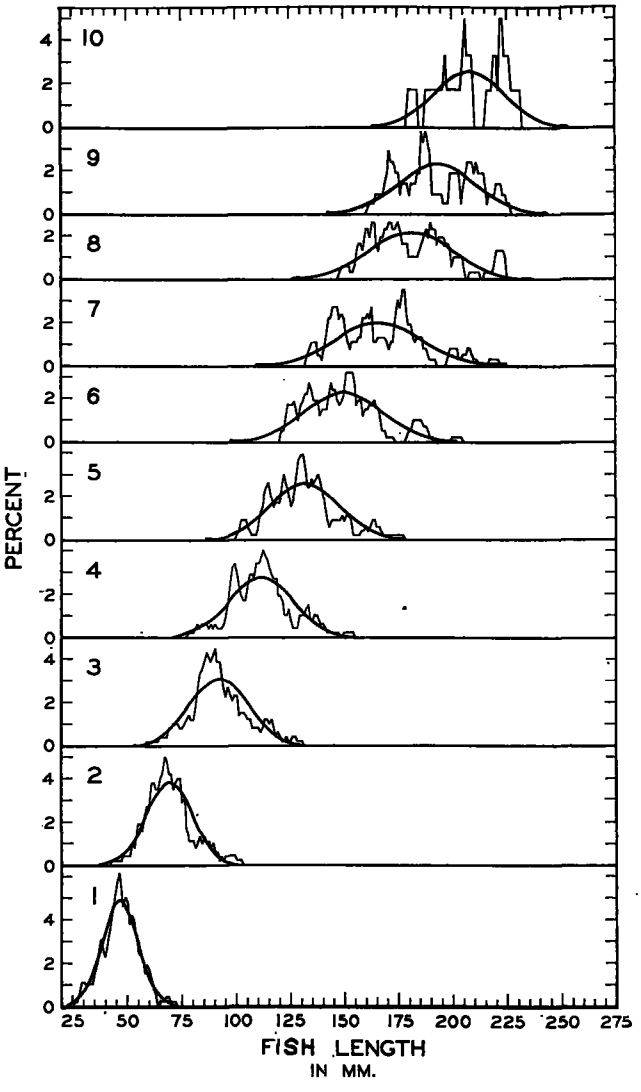

FIGURE 20.—Length-frequency distributions of rosefish from the Browns Bank area of western Nova Scotia for each annulus of annuli 1–10. Lightly drawn irregular curves are the actual frequency distributions smoothed by a moving average of five. Heavily drawn smooth curves are the normal curves fitted to the actual frequency data.

Maine. The size at the first annulus is 47 mm.; annulus 2, 69 mm.; annulus 3, 92 mm.; annulus 4, 112 mm.; annulus 5, 132 mm.; annulus 6, 150 mm.; annulus 7, 167 mm.; annulus 8, 181 mm.; annulus 9, 193 mm.; annulus 10, 208 mm. (table 11, fig. 20).

COMPARISON OF THE ACTUAL AND CALCULATED AVERAGE LENGTH AT ANNULUS 1

The accuracy of the calculated average length of rosefish at annulus 1 is indicated by a comparison with the actual average length of a series of fish

TABLE 10.—*Calculated fish length, in millimeters, at each annulus to the ninth annulus of rosefish taken in the Gulf of Maine*

[Calculations [1] based on method 2]

Fish length, in millimeters	Annulus								
	1	2	3	4	5	6	7	8	9
30–34	1								
35–39	10								
40–44	36								
45–49	78	1							
50–54	62	2							
55–59	60	16							
60–64	33	22							
65–69	23	42	1						
70–74	5	56	8						
75–79		46	10						
80–84		45	18						
85–89		41	32	1					
90–94		17	28	8					
95–99		4	32	13					
100–104		3	30	17	2				
105–109		2	30	17	2				
110–114			24	18	3				
115–119			17	25	10	2			
120–124			9	24	10	1			
125–129			5	16	19	2	1		
130–134			4	20	12	7	1		
135–139			1	13	13	6	1		
140–144			1	13	14	12	1		
145–149			1	5	13	8	4		
150–154				4	14	8	3		
155–159				2	13	8	1		
160–164				5	6	7	2	1	
165–169					4	7	4	2	
170–174				1	2	14	3		
175–179				1		6	2	1	
180–184					1		5		
185–189						1	5		
190–194					1	1	3	3	
195–199							1	1	
200–204								3	1
205–209							1	1	
210–214									
215–219									
220–224									1
225–229									
230–234									1
Total number of fish	308	297	251	203	139	90	38	12	3
Mean	52	76	99	121	139	154	169	189	218
Standard deviation	7.9	10.5	14.6	17.4	16.9	16.7	19.5	16.5	

[1] Calculations were based on a curve fitted to the values for fish lengths and scale radii obtained from material collected throughout the Gulf of Maine from September 1942 through August 1943 (collections 1–18; 269 fish). Data collected throughout the Gulf of Maine in 1942 (collections 1, 3, 4, 6; 113 fish); in 1943 (collections 10, 11, and 13–18; 131 fish); and in 1944 (collections 25–39; 65 fish) were analyzed using this curve. 1 fish born in 1932 is not included in the above data.

showing one annulus on their scales. Sixty-one specimens, the total catch of rosefish taken incidentally by a shrimp trawler fishing in the Monhegan-Jeffreys-Platts area in March 1947, ranged in size from 46 to 63 mm. and averaged 56 mm. in length. Scales from 12 of these fish taken at random had 1 annulus, with 2 of the 12 showing initial growth toward the second annulus. The calculated length of rosefish at annulus 1 in the Gulf of Maine has been established as 52 mm. which is in close agreement with the 56-mm. length obtained above.

GROWTH BETWEEN ANNULI

The rate of growth of rosefish from the Gulf of Maine and off the Browns Bank area of western Nova Scotia was computed by averaging the differences between the calculated lengths of individual fish at each annulus. For the Gulf of Maine data, the growth rate between annuli of individual year classes was determined separately (table 12). The average growth between annuli shows little variation within year classes. The average rate of growth for all year classes to annulus 1 is 52 mm.; between annulus 1 and 2, 24 mm.; 2 and 3, 24 mm.; 3 and 4, 22 mm.; 4 and 5, 19 mm.; 5 and 6, 19 mm.; and between 6 and 7, 7 and 8, 8 and 9, 16 mm. (table 13, fig. 21).

In the Browns Bank area of western Nova Scotia, the average growth to annulus 1 is 47 mm.; between annulus 1 and 2, 22 mm.; annulus 2 and 3, 23 mm.; annulus 3 and 4, 21 mm.; 4 and 5, 20 mm.; 5 and 6, 19 mm.; between 6 and 7, 7 and 8, 8 and 9, 17 mm.; and between 9 and 10, 16 mm. (table 14, fig. 21).

TABLE 11.—*Calculated fish length, in millimeters, at each annulus to the eleventh annulus of rosefish taken in the Browns Bank area of western Nova Scotia*

[Calculations [1] based on method 1]

Fish length, in millimeters	Annulus										
	1	2	3	4	5	6	7	8	9	10	11
25–29	1										
30–34	5										
35–39	13										
40–44	18										
45–49	28	1									
50–54	22	5									
55–59	11	8									
60–64	4	20	1								
65–69	1	26	2								
70–74	1	20	5								
75–79		9	6								
80–84		5	13	3							
85–89		6	21	2							
90–94		1	20	2							
95–99		2	12	12							
100–104		1	8	9	4						
105–109			4	14	1						
110–114			4	19	7						
115–119			4	13	7						
120–124			1	5	14	2					
125–129			2	2	10	8					
130–134				6	15	9					
135–139				5	13	8	4				
140–144				1	4	6	5				
145–149				1	4	8	10				
150–154				1	5	13	4	2			
155–159					1	8	5	5			
160–164					3	7	8	6	1		
165–169					2	4	5	6	2		
170–174					1	1	4	8	5		
175–179					1		13	5	3		
180–184						4	5	3	3	1	
185–189						3	3	6	7		
190–194							1	7	2	1	
195–199								5	1	2	
200–204						1	3	3	4	1	
205–209							3		5	2	
210–214								1	4		
215–219							1	1	2	1	
220–224								4	3	3	
225–229										1	1
230–234											
Total number of fish	104	104	103	95	92	82	74	62	42	12	1
Mean	47	69	92	112	132	150	167	181	193	208	225
Standard deviation	8.2	10.4	12.9	14.1	15.5	17.3	19.5	18.6	17.0	15.0	----

[1] Based on a straight line fitted to the logarithmic values for fish lengths and scale radii obtained from material collected from December 1942 through December 1943 in the Browns Bank area (collections 40–48; 111 fish). 7 fish could not be read because no good scales were available.

TABLE 12.—*Average calculated growth, in millimeters, between annuli of rosefish captured in the Gulf of Maine* [1]

[Calculations [2] based on method 2]

Growth in year [3]	Annulus								
	0–1 [4]	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9
1933 [5]	48	31	25	8	21	13	17	23	9
1934	52	23	23	22	21	17	16	18	16
1935	51	24	21	20	17	18	16	15	
1936	55	22	22	21	18	20	15	12	
1937	50	26	26	21	22	19	14		
1938	52	26	26	21	20	16			
1939	51	24	25	22	22				
1940	52	24	22	28					
1941	54	21	28						
1942	58	26							
1943	55								
Weighted mean	52	23	24	22	19	19	16	16	16
Standard deviation	7.92	8.91	8.79	7.24	6.01	6.01	4.42	6.78	
Number of fish used	308	297	251	203	139	90	38	12	3

[1] Includes materials collected in 1942 (collections 1, 3, 4, 6: 113 fish); in 1943 (collections 10, 11, and 13–18: 131 fish); and in 1944 (collections 25–39: 65 fish). Data combined for years 1942, 1943, and 1944.

[2] Data collected throughout the Gulf of Maine from September 1942 through August 1943 (collections 1–18: 269 fish) were used in deriving the curve employed in obtaining calculated lengths at each annulus by means of method 2.

[3] Extends from April of the indicated year through March of the following year, as shown by the study of time of annular band formation.

[4] This includes the size at birth, growth until scale formation, and subsequent growth until the completion of the first annulus. Spawning occurs from mid-May through early September, and scales are formed in the following year. The first annular ring forms in the second year after the birth of the fish.

[5] Only 1 fish was available, and it has not been included in the statistical calculations.

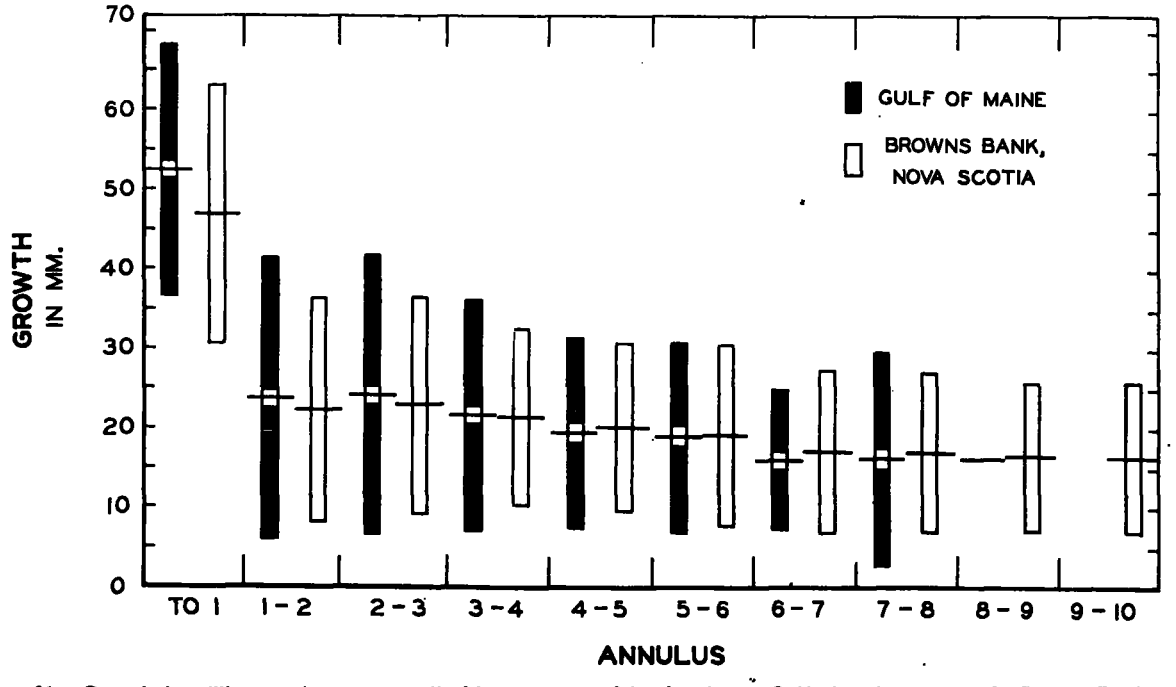

FIGURE 21.—Growth, in millimeters, between annuli of immature rosefish taken in the Gulf of Maine and off the Browns Bank area of western Nova Scotia. The horizontal lines represent the average growth to each annulus and the vertical bars two standard deviations above and below the mean.

TABLE 13.—*Calculated growth, in millimeters, per annulus to the ninth annulus of rosefish taken in the Gulf of Maine*

[Calculations [1] based on method 2]

Growth to first annulus		Growth between annuli								
Millimeters	Number of fish	Millimeters	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9
			Number of fish							
34	1	5	-------	-------	-------	-------	-------	-------	-------	-------
35	-------	6	-------	1	-------	-------	-------	-------	-------	-------
36	3	7	-------	-------	1	-------	3	2	-------	-------
37	2	8	1	1	2	2	1	-------	-------	-------
38	2	9	3	1	3	1	2	-------	1	-------
39	3	10	4	1	-------	3	1	2	2	-------
40	3	11	9	1	4	6	1	-------	-------	1
41	8	12	12	3	2	6	2	1	1	1
42	8	13	11	9	10	7	4	3	1	-------
43	7	14	8	10	13	6	5	5	2	-------
44	10	15	17	9	7	7	9	6	-------	-------
45	16	16	10	17	10	8	4	6	1	-------
46	14	17	5	11	13	12	11	2	1	-------
47	15	18	15	13	13	5	7	2	-------	-------
48	14	19	9	15	19	10	2	4	-------	-------
49	19	20	11	8	8	8	5	1	-------	-------
50	11	21	14	15	13	13	3	-------	-------	-------
51	16	22	16	15	7	5	7	-------	-------	-------
52	13	23	14	13	2	8	5	1	-------	-------
53	10	24	14	7	7	8	2	-------	1	-------
54	12	25	13	9	6	4	4	1	-------	-------
55	15	26	9	8	9	5	1	1	-------	1
56	19	27	9	7	11	2	3	-------	-------	-------
57	11	28	3	2	10	3	1	-------	2	-------
58	5	29	15	7	3	3	1	1	-------	-------
59	10	30	7	4	2	1	1	-------	-------	-------
60	7	31	11	11	3	1	3	-------	-------	-------
61	6	32	7	5	4	1	-------	-------	-------	-------
62	8	33	7	9	2	-------	2	-------	-------	-------
63	6	34	3	7	6	1	-------	-------	-------	-------
64	6	35	6	1	4	1	-------	-------	-------	-------
65	8	36	4	5	2	1	-------	-------	-------	-------
66	9	37	9	2	3	-------	-------	-------	-------	-------
67	4	38	2	2	3	-------	-------	-------	-------	-------
68	1	39	4	-------	-------	1	-------	-------	-------	-------
69	1	40	5	5	1	-------	-------	-------	-------	-------
70	-------	41	2	5	-------	-------	-------	-------	-------	-------
71	2	42	2	2	-------	-------	-------	-------	-------	-------
72	1	43	-------	4	-------	-------	-------	-------	-------	-------
73	1	44	1	3	-------	-------	-------	-------	-------	-------
74	1	45	-------	-------	-------	-------	-------	-------	-------	-------
75	-------	46	1	-------	-------	-------	-------	-------	-------	-------
76	-------	47	-------	1	-------	-------	-------	-------	-------	-------
77	-------	48	2	1	-------	-------	-------	-------	-------	-------
78	-------	49	-------	-------	-------	-------	-------	-------	-------	-------
79	-------	50	-------	1	-------	-------	-------	-------	-------	-------
80	-------	51	1	-------	-------	-------	-------	-------	-------	-------
81	-------	52	-------	-------	-------	-------	-------	-------	-------	-------
82	-------	53	-------	-------	-------	-------	-------	-------	-------	-------
83	-------	54	-------	-------	-------	-------	-------	-------	-------	-------
84	-------	55	1	-------	-------	-------	-------	-------	-------	-------
Total number of fish	308	------	297	251	203	139	90	38	12	3
Mean	52.42	------	23.72	24.15	21.62	19.40	18.86	16.05	16.25	16.33
Standard deviation	7.92	------	8.91	8.79	7.24	6.01	6.01	4.42	6.76	-------

[1] Based on a curve fitted to the values for fish lengths and scale radii obtained from material collected throughout the Gulf of Maine from September 1942 through August 1943 (collections 1–18; 269 fish). Data collected throughout the Gulf of Maine in 1942 (collections 1, 3, 4, 6; 113 fish); in 1943 (collections 10, 11, and 13–18; 131 fish); and in 1944 (collections 25–39; 65 fish) were analyzed using this curve. 1 fish born in 1932 has not been included in the above analysis.

TABLE 14.—*Calculated growth, in millimeters, per annulus to the eleventh annulus of rosefish taken in the Browns Bank area of western Nova Scotia*

[Calculations[1] based on method 1]

Growth to first annulus		Growth between annuli											
Millimeters	Number of fish	Millimeters	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11
			Number of fish									
28	1	5	-----	-----	-----	-----	-----	1	-----	-----	-----	-----
29	-----	6	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
30	2	7	-----	-----	-----	-----	-----	1	-----	-----	1	-----
31	3	8	-----	-----	-----	-----	1	-----	1	1	-----	-----
32	-----	9	1	-----	-----	1	1	1	-----	-----	-----	-----
33	-----	10	1	-----	-----	1	-----	5	2	3	-----	-----
34	-----	11	-----	2	-----	3	2	3	5	3	1	-----
35	2	12	3	3	1	2	6	1	5	3	-----	-----
36	3	13	3	2	4	1	2	5	7	1	1	-----
37	3	14	6	3	3	5	6	7	5	5	1	-----
38	2	15	4	3	8	5	6	5	4	4	-----	-----
39	3	16	6	4	5	7	8	3	3	3	1	-----
40	5	17	6	9	7	8	8	6	1	2	1	-----
41	-----	18	4	4	7	4	5	8	3	2	3	-----
42	2	19	6	6	6	8	6	6	6	3	1	-----
43	5	20	6	7	3	6	4	10	6	4	-----	-----
44	6	21	7	4	6	5	1	-----	-----	1	1	-----
45	9	22	7	8	5	6	5	3	5	1	-----	1
46	3	23	5	6	8	7	5	2	2	2	-----	-----
47	6	24	3	5	7	2	-----	1	3	-----	-----	-----
48	8	25	3	4	2	5	-----	1	-----	4	1	-----
49	2	26	3	4	7	3	2	1	3	-----	-----	-----
50	5	27	6	2	2	-----	2	2	-----	-----	-----	-----
51	5	28	4	3	3	7	5	-----	-----	-----	-----	-----
52	5	29	5	4	2	1	5	-----	-----	-----	-----	-----
53	3	30	2	2	-----	4	-----	1	-----	-----	-----	-----
54	4	31	3	5	3	-----	1	-----	-----	-----	-----	-----
55	4	32	5	4	1	1	-----	-----	1	-----	-----	-----
56	1	33	-----	1	4	-----	1	1	-----	-----	-----	-----
57	1	34	1	1	-----	-----	-----	-----	-----	-----	-----	-----
58	2	35	-----	1	-----	-----	-----	-----	-----	-----	-----	-----
59	3	36	-----	3	1	-----	-----	-----	-----	-----	-----	-----
60	1	37	-----	1	-----	-----	-----	-----	-----	-----	-----	-----
61	3	38	1	-----	-----	-----	-----	-----	-----	-----	-----	-----
62	-----	39	-----	2	-----	-----	-----	-----	-----	-----	-----	-----
63	-----	40	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
64	-----	41	1	-----	-----	-----	-----	-----	-----	-----	-----	-----
65	-----	42	1	-----	-----	-----	-----	-----	-----	-----	-----	-----
66	-----	43	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
67	1	44	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
68	-----	45	1	-----	-----	-----	-----	-----	-----	-----	-----	-----
69	-----	----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
70	1	----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Total number of fish	104	----	104	103	95	92	82	74	62	42	12	1
Mean	46.91	----	22.26	22.89	21.41	20.13	19.07	17.11	17.02	16.52	16.42	22.00
Standard deviation	8.15	----	7.06	6.80	5.62	5.33	5.75	5.15	5.05	4.69	4.72	-----

[1] Based on a straight line fitted to the logarithmic values for fish lengths and scale radii obtained from material collected from December 1942 through December 1943 (collections 40–48; 111 fish). The scales from 7 fish could not be read because no good scales were available).

CONCLUSIONS

Compared with other North Atlantic species of commercial importance such as haddock, cod, and mackerel, the rosefish is extremely slow growing, averaging less than a 25-mm. increase in length per annulus to the ninth annulus in both the Gulf of Maine and off the Browns Bank area of western Nova Scotia. Since these results were obtained for primarily immature fish, it is to be expected that the mature fish will have a slower rate of growth. Marketable rosefish, those 200 mm. in length or greater, are mostly more than 10 years of age, and a superficial examination of the scales of the larger fish indicate that many must be 20 or more years old. A comparable slow rate of growth is reported for rosefish in the Barents Sea. Veschezerov (1941) presents data which show an average growth of 27.8 mm. per annulus to the ninth annulus for fish in that region.

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UNITED STATES DEPARTMENT OF THE INTERIOR, J. A. KRUG, *Secretary*
FISH AND WILDLIFE SERVICE, ALBERT M. DAY, *Director*

NOTES ON THE PHILIPPINE FRIGATE MACKERELS FAMILY THUNNIDAE, GENUS *AUXIS*

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Notes on the Philippine Frigate Mackerels, Family Thunnidae, Genus *Auxis*

The frigate mackerel (genus *Auxis*) is a food fish of some importance in the Republic of the Philippines, although it is of little economic importance throughout much of the world. While collecting biological data on the more common commercial fishes of the Philippines for the pelagic fish-studies section of the Philippine Fishery Program of the Fish and Wildlife Service,[1] it was found that the commercial catch of *Auxis* is composed of two species. Inasmuch as the relative importance of each to the catch is not known, this paper is an effort to define the distinguishing characteristics of the two forms as a basis for securing such information. The existence of two species was first suggested by Dr. Earl S. Herald, formerly aquatic biologist, Philippine Fishery Program, while investigating the commercial fisheries of Batangas, Luzon.

The genus *Auxis* is badly in need of systematic revision on a world-wide basis, but, in the absence of adequate museum collections and library facilities, no attempt is made here to clarify the confused taxonomic relationships. Rather than further increase the chaos of species, the names *Auxis tapeinosoma* Bleeker and *Auxis thazard* (Lacépède), as used by Dr. A. W. Herre, formerly ichthyologist, Philippine Fishery Program, in his check-list of Philippine fishes,[2] have been retained as a matter of convenience. This specific nomenclature, while perhaps subject to question, serves to identify the Philippine species of this genus sufficiently for present purposes. Further changes in nomenclature at this time would only add to the confusion which surrounds this genus. It is hoped that the data assembled here will be of value to investigators, and aid in future biological and systematic studies.

[1] A part of the Philippine Rehabilitation Program authorized by the Philippine Rehabilitation Act of 1946, title 50, Apo. U. S. Code, Sec. 1789.

[2] Unpublished manuscript.

Family THUNNIDAE

Genus *AUXIS* Cuvier

Auxis Cuvier, 1829, Règne Animal, Ed. II, II, p. 199 (type *Scomber rochei* Risso = *Scomber thazard* Lacépède)

Body robust, fusiform, almost cylindrical in cross section, only slightly compressed. Head large, tapering rapidly to a pointed snout. Mouth moderate, oblique, end of maxillary not covered by preorbital. Teeth small, pointed, present on jaws. Occasionally few teeth on vomer. Gill rakers, close set, long, and slender. Lateral line without a distinct arch, slightly curved and with small undulations. Caudal peduncle with small lateral keels. Body scaled anteriorly, forming a corselet. Corselet with a posterior prolongation of scales along lateral line. Fins small, first dorsal fin roughly triangular in shape and not continuous or closely adjoining second dorsal. Second dorsal and anal each followed by 8 and 7 finlets.

The genus *Auxis* is found in most tropical and temperate waters throughout the world. In Philippine waters Dr. Herre (1940) has recorded *Auxis thazard* from Nasugbu, and Balayan Bay, Batangas Province, Luzon, and in 1931 from Jolo, Sulu Province. Recent records made by biologists of the Philippine Fishery Program include, in addition to the above localities: Maya, Danao, and Cebu City, Cebu Island; Bohol Island; Zamboanga City, Davao, and Margosatubig, Mindanao; and Iloilo City, Panay Island. Previously *Auxis tapeinosoma* has never been recorded from the Philippines, but during the past year specimens have been collected at Siocon Bay and Zamboanga City, Mindanao, and Batangas Bay, Luzon. Dr. A. W. Herre in his check-list of Philippine fishes places a record of *Auxis thazard* from Culion, Philippines, 1931, in synonomy with *Auxis tapeinosoma*. Undoubtedly,

an expanded program of studying the composition of catches in local markets would reveal their presence throughout most of the Philippines.

Locality records for *Auxis thazard* other than the Philippines include the Hawaiian Islands, Sea of Japan, west coast of North America, the Mediterranean Sea, and the Atlantic Ocean. The second species under consideration, *Auxis tapeinosoma*, has been recorded from Japan and the Dutch East Indies.

Key to the Genus *Auxis* [3]

1a. First dorsal continuous or almost continuous with second dorsal; axillary scales between ventral fins small, about one-half length of fins.....(Thunnidae except *Auxis*)

1b. First dorsal not continuous or almost continuous with second dorsal.

Interspace between fins almost equal to length of head. Axillary scales between ventral fins equal in length to fins Genus *Auxis*

2a. Corselet scales along lateral line 2 to 4 irregular scale rows wide under origin of second dorsal. Corselet abruptly tapering to narrow band of 3 to 4 scales along lateral line at about midway between first and second dorsals. Total gill-raker count of first gill arch 37 to 43.....*Auxis thazard* (Lacépède)

2b. Corselet scales along lateral line in a wide band 7 to 12 irregular scale rows wide under origin of second dorsal. Corselet tapers gradually and evenly throughout length, ends under about second dorsal finlet. Total gill-raker count of first gill arch 44 to 48.....*Auxis tapeinosoma* Bleeker

There is considerable disagreement among taxonomists as to the number of valid species in this genus. Some believe there is a single world-wide species (*Auxis thazard*), while others are of the opinion that one or more additional species are to be found. It is quite evident, however, from the data at hand that two species occur in the Philippines. A survey of the available literature shows that possibly two seemingly similar species occur in the eastern Pacific area. Comparison of two descriptions of specimens of this genus (Meek and Hildebrand 1923; and Fowler 1938) reveals that the authors were describing two entirely different species. Fowler's description based on two specimens from the Galapagos Islands off the west coast of South America agrees with *Auxis tapeinosoma* as defined here, having the elongate posterior prolongation of the corselet along the lateral line and the increased gill-raker count. The description by Meek and Hildebrand based upon a composite collection of six specimens from Woods Hole, Mass., Hawaii, and Java agrees in gill-raker count of the lower gill arch with *Auxis thazard* as named here. The specimen used by Walford (1937) to illustrate *Auxis thazard* is clearly identifiable as *A. tapeinosoma* with its long, posterior extension of the corselet along the lateral line. It is not known whether the eastern Pacific forms are identical with the species occurring in Philippine waters, and a careful study of a considerable number of collections will be necessary before this can be ascertained.

Two additional species of frigate mackerel, *Auxis hira* and *A. maru*, were described from Japanese waters by Kishinouye (1915). The description of the larger of the two Japanese species (*Auxis hira*) agrees very well with specimens of Philippine *Auxis thazard* as determined by Drs. Herre and Herald. Until specimens from Japan are available for comparison *hira* is provisionally placed in synonomy with *thazard*. The second, smaller species from Japan, *Auxis maru*, seems identical with that which Dr. Herre provisionally names *A. tapeinosoma* and is tentatively placed in synonomy with it.

[3] This key adapted from a memorandum to field biologists, Philippine Fishery Program, prepared by Dr. Earl S. Herald.

[4] Fork length is defined as the length from the tip of the snout to the end of the median caudal rays.

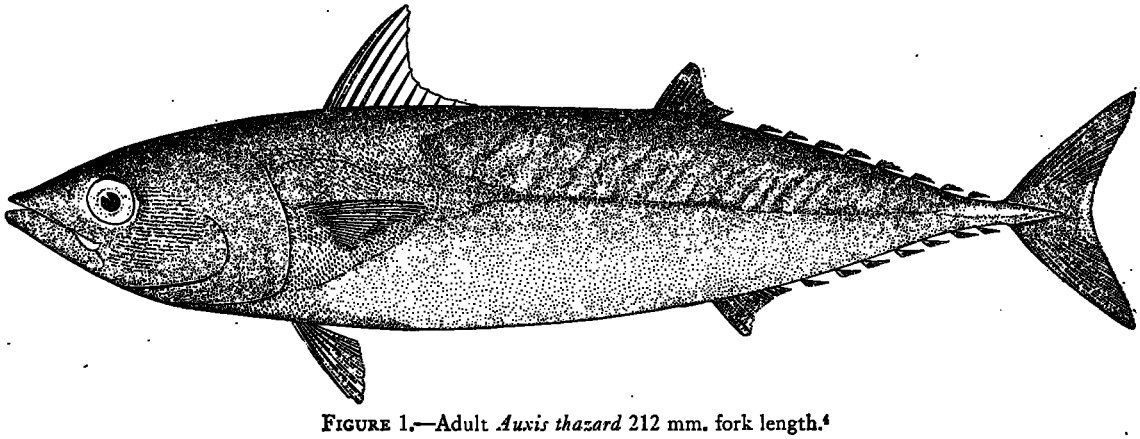

FIGURE 1.—Adult *Auxis thazard* 212 mm. fork length.[4]

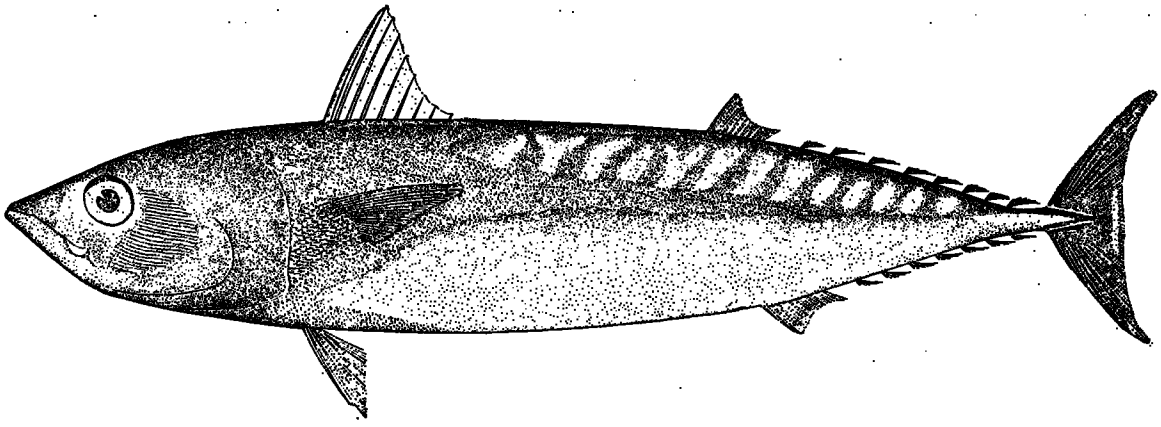

FIGURE 2.—Adult *Auxis tapeinosoma*, 228 mm. fork length.

Auxis thazard (Lacépède)

Scomber thazard Lacépède, 1802, vol. 3, p. 9 (type locality between 6° and 7° S. latitude, off coast of New Guinea).
?*Auxis hira* Kishinouye, 1915, Susan Gakkai Ho. I, p. 23, plate 1, fig. 16 (Japan).

Body robust, sides flattened, slightly compressed. Dorsal outline broadly and evenly curved, ventral outline flattened abdominally. Depth 3.89 to 5.75 in standard length; [5] depth increases gradually as fish becomes larger.

Head large, 3.95 to 4.35 in standard length. Snout short, pointed, longer than eye diameter, 3.3 to 3.6 in head. Mouth moderate, oblique, end of maxillary reaches to or slightly past vertical from anterior edge of pupil. End of maxillary not hidden beneath edge of preorbital. Jaws equal or lower jaw slightly projecting in larger specimens. Single row of small, pointed teeth on both jaws. Palatine teeth absent, occasionally a few small, scattered teeth on vomer. Eyes moderate, placed high on sides of head, 4 to 5.14 in head. Interorbital wider than eye, somewhat flatly rounded. Branchiostegal rays, 7. Gill membranes not united, free from isthmus. Gill rakers, long and slender, 9–10+1+27–32 on first gill arch.

Dorsal fins two, separated by interspace slightly shorter than head length. First dorsal roughly triangular, X to XII (mostly XI to XII). Anterior spine longest, equal to fin base. Second dorsal small, 10 to 12 (mostly 11 to 12) rays. Dorsal finlets, 8. Anal fin small, II, 8 to 11, origin under last ray of second dorsal. Anal finlets, 7 (8 in one specimen). Pectoral fin short, roughly triangular, tip of fin reaches almost to end of first dorsal base. Ventral fins thoracic. Axillary scales equal ventrals in length.

Body naked except for a corselet of scales anteriorly. Corselet scales large and imbricated above pectoral base. Corselet extends posteriorly along lateral line, tapering abruptly to a narrow band about halfway between end of first dorsal and origin of second. Only 2 to 4 irregular scale-rows wide at second dorsal origin. Caudal peduncle small, lateral keels poorly developed. Lateral line without a distinct arch and more or less undulating.

Color of formalin-preserved specimens: dorsally deep brown or blackish becoming slightly paler laterally. Abdomen and lower portion of sides pale, sometimes light brown or gray. Sides above and behind corselet with elongate irregular, oblique black bars. First dorsal light brown along anterior spines. Other fins almost colorless.

The following material was examined: 24 specimens, 103.7 to 367 mm. standard length, Batangas Public Market, Batangas, Luzon, July 1, 1948; 4 specimens, 170 to 204.6 mm. standard length, Zamboanga City Market, Zamboanga, Mindanao, February 28, 1948. A series of measurements adapted from Godsil and Byers (1944) was made on these specimens. A summary of these measurements is given in table 1.

Auxis tapeinosoma Bleeker

Auxis tapeinosoma Bleeker, 1854, p. 408 (Nagasaki, Japan).
? *Auxis maru* Kishinouye, 1915, p. 24, plate 1, fig. 19 (Japan).

Body robust, rounded, almost cylindrical in cross section. Dorsal outline moderately and evenly curved. Ventral outline similar, but slightly flattened in abdominal region. Depth 5.3 to 6.1 in standard length.

[5] Standard length is defined as the length from the tip of the snout to the end of the hypural plate.

Head moderate, 4.35 to 4.51 in standard length. Snout short, pointed, slightly longer than eye diameter, 3.3 to 3.5 in head. Mouth moderate, oblique, 2.5 to 2.69 in head. End of maxillary reaching to slightly before or behind vertical from anterior margin of eye. End of maxillary not hidden beneath edge of preorbital. Jaws equal, single row of small, pointed teeth on jaws. Palatine teeth absent, occasionally few small teeth on vomer. Eye moderate, 4.2 to 4.8 in head. Interorbital flattened, width equal eye diameter. Branchiostegal rays, 7.

TABLE 1.—*Measurements, in millimeters, and counts of individual specimens of* Auxis thazard (*Lacépède*)

Specimen No.	Standard length	Fork length	Head length	Snout to first dorsal insertion	Snout to second dorsal insertion	Snout to anal insertion
1	103.7	109	24	32	65	69
2	110.5	116.2	28	37	69.5	76
3	115.5	122	28.5	37	73	79
4	118	124	28.5	37.5	74	78
5	121.5	127.5	29.2	37.6	75	80.8
6	123	128.5	29.5	38.6	78	83.2
7	135.4	140.2	32.5	42.1	82.9	91
8	135.5	140.6	33	43	83	90.5
9	137.4	144	33	43.2	84	92
10	139	145	33.5	44.1	85	94
11	142	147.9	33.5	44.5	88	95.2
12	142	147	35	43.8	88	96
13	142.5	148.5	34.7	45.6	89	93.3
14	143.2	149.4	33.5	45.1	88	95.5
15	144.5	150	34	46.2	90.1	95.6
16	144.5	150	33.1	45.2	89	96
17	151	156	35.1	46.8	93.5	101
18	154	159	35.6	49	100.4	100
19	156.7	162	37.5	49	95.2	104
20	170	176.9	40.4	53.1	104	111.9
21	182.8	188.7	43.9	56.8	113	124.1
22	186.4	193	43	58.2	115.1	126.1
23	196	204.6	46.7	62.3	122.7	134.5
24	301.5	315	75.2	109.8	196.5	213.6
25	326.9	337	80.5	106.7	216	240.9
26	334.6	346	80.6	108	213	238.9
27	338	350	83.4	110	231.1	245.5
28	367	377	89.4	119	234.5	264.8

Specimen No.	Depth	Pectoral base to first dorsal insertion	Length first to second dorsal insertion	Pectoral length	Length first dorsal base
1	18	9	33.5	10	16
2	21	11.5	35.2	10.8	18.5
3	23	13	35	12	18
4	23	12.5	37.7	11	17
5	24.9	12.5	38.2	12.8	20.5
6	24	13	39.5	12.5	20.5
7	25.7	14.1	43	14.1	18.2
8	26	14.2	42.6	14.5	19.2
9	28	14	43.5	14	20
10	25.8	15	43.2	14	20.2
11	28.5	15.2	46	14.8	24.5
12	29	16	45	14.8	23
13	27.8	15	46.2	14.2	21.6
14	28.1	15.9	45.9	14.9	21
15	29.1	15.1	45.2	15	20
16	28.2	15	45	14.7	20.5
17	29.2	17	48.2	14.6	22
18	31.1	17.4	48	16.5	22.5
19	32	18.2	49	16.9	26.1
20	31	18	56.4	18.1	23.2
21	34.3	17.8	56.1	20.2	28.7
22	34.2	19.7	58.8	21.6	27.5
23	43.1	21	62.1	21.9	27.9
24	74.2	38	98.2	40.5	39.9
25	84.2	40.1	109.8	47	42.4
26	84.1	42.4	105.5	45.4	44
27	85	42.8	112	51.6	46.9
28	88	47.8	116.2	54.9	48.9

TABLE 1.—*Measurements, in millimeters, and counts of individual specimens of* Auxis thazard (*Lacépède*)—Continued

Specimen No.	Length second dorsal base	Length anal base	Eye diameter	Maxillary length	First dorsal rays
1	5	5.2	6	10	12
2	6	6.2	6.5	12	12
3	6	6	6.5	12	11
4	6.2	6	6.5	12	11
5	7.7	7.2	7	12.1	11
6	7	7.2	7	12	12
7	8.3	8.1	7.2	13	11
8	8	8.2	7.7	13.3	11
9	8.5	8.8	7.5	13.1	11
10	8.8	9	7.5	13.6	11
11	8.6	8.5	7.4	14.2	11
12	9	8.6	7.5	13.8	11
13	9.1	9	7.2	13.2	11
14	9	9.1	7.9	13.4	11
15	9.1	9	7.3	13.8	11
16	9.2	8.5	7.5	14	11
17	9	9.5	8	14.7	11
18	10.5	9.5	8	14.5	11
19	9.5	10.5	7.9	14.7	10
20	11.1	10	8.2	15.7	11
21	11	10.9	9.4	17	12
22	12.5	10.6	9.8	17.1	11
23	10.8	11.2	9.9	18.4	11
24	19.3	16	15	28.8	10
25	18.8	20.3	16.1	30.9	10
26	20	18.1	16.2	30.9	10
27	19.9	20.2	17.4	31	10
28	21	20.4	17.2	33.6	10

Specimen No.	Second dorsal rays	Dorsal finlets	Anal finrays	Anal finlets	Gill rakers
1	11	8	11	7	9+1+29
2	10	8	13	7	10+1+29
3	11	8	10	7	8+1+28
4	11	8	10	7	9+1+29
5	11	8	12	7	10+1+31
6	10	8	13	7	10+1+27
7	11	8	12	7	10+1+30
8	12	8	13	7	10+1+30
9	11	8	13	7	9+1+30
10	12	8	12	7	9+1+32
11	12	8	12	7	10+1+30
12	12	8	12	7	10+1+28
13	11	8	12	7	10+1+30
14	12	8	13	7	10+1+28
15	11	8	14	7	10+1+30
16	12	8	13	7	10+1+30
17	12	8	13	7	10+1+30
18	12	8	13	7	10+1+32
19	10	8	14	7	10+1+30
20	11	8	13	7	9+1+30
21	11	8	14	7	9+1+29
22	11	8	13	7	10+1+30
23	11	8	14	7	8+1+30
24	12	8	13	7	9+1+29
25	11	8	14	7	10+1+31
26	11	8	12	8	9+1+30
27	11	8	13	7	11+1+31
28	11	8	13	7	10+1+29

Gill membranes not united, free from isthmus. Gill rakers long and slender, 10–12+1+31–35.

Dorsal fins two, first dorsal X to XI, roughly triangular, anterior spine longest, almost equal to base of fin. Second dorsal small, 10 to 12 (mostly 11) rays. Dorsal finlets, 7 (8 in one specimen). Anal fin small, II, 10 to 12, origin at vertical through last ray of second dorsal. Anal finlets, 7. Pectoral fin roughly triangular, tip of fin more or less reaches end of first dorsal base, 8.95 to 9.91 in standard length. Ventral fins thoracic, axillary scales long, equal to ventral fin.

Body naked except for corselet of scales anteriorly. Scales large and imbricated above pectoral base. Corselet extends posteriorly along lateral line, tapering gradually and ending under about second dorsal finlet. Corselet, 7 to 12 irregular scale rows wide at vertical through second dorsal origin. Caudal peduncle small, lateral keels poorly developed. Lateral line without distinct arch, more or less undulating.

Color of specimens preserved in formalin: dark brown or black dorsally, slightly lighter laterally. Abdomen and lower part of sides pale. Sides above and behind corselet with elongate, black spots or more or less wavy bars. First dorsal with light brown along anterior spines, remainder of fins more or less colorless.

The following material was examined: 21 specimens, 122 to 231 mm. standard length, Batangas Public Market, Batangas, Luzon, July 2, 1948; 7 specimens, 186 to 199 mm. standard length, Zamboanga Public Market, Zamboanga City, Mindanao, February 28, 1949. A series of measurements similar to those made on *Auxis thazard* were made and are tabulated in table 2.

TABLE 2.—*Measurements, in millimeters, and counts of individual specimens of* Auxis tapeinosoma *Bleeker*

Specimen No.	Standard length	Body length	Head length	Snout to first dorsal insertion	Snout to second dorsal insertion	Snout to anal insertion
1	122	126.7	27.7	36.5	76.1	83.4
2	129	134.1	29.6	39.7	82.5	89
3	161.9	167.5	38.5	47.3	102.5	112.2
4	186.9	193	41.6	57	118.8	129.4
5	190	196.7	43.1	56.2	122	132
6	191.9	186.1	41.2	54.9	118.1	128.8
7	192	199.5	43.6	57.9	124.2	133
8	192.5	200.8	44.2	59.1	124	135
9	196.2	205	44	58.8	126.4	136.6
10	199.1	207.5	44.1	60.1	125.6	138.1
11	215	221.8	51.9	69.7	137.3	150
12	215	224	52	68.8	140.4	154
13	215.9	222.5	51.4	69	144.2	147.5
14	217	224	52.7	69.2	140.5	150.1
15	217.4	223.5	51.1	67.9	139	152.5
16	218	224.1	52.9	69.2	139.9	153
17	219.8	228	52.8	70.1	145	155.5
18	220.2	227.1	51.8	69.9	142.1	149.1
19	221	228.7	52.2	70.1	144	154
20	221.1	225.8	54	70.4	141	153.2
21	222	229	54.6	73.1	147.5	152.1
22	222.2	230.3	54.4	71.4	145	154.5
23	222.4	230.1	54.9	70	147.8	159.9
24	222.8	231	52.4	67.5	144.9	156.8
25	222.9	228.1	52.1	68	142.2	154
26	225	233	53.9	70.9	145.3	157.9
27	228	235.2	52.9	70	148	161.2
28	231	237	54.2	73.1	152.2	160.2

Specimen No.	Depth	Pectoral base to first dorsal insertion	Length first to second dorsal origin	Pectoral length	Length first dorsal base
1	20.2	11.2	41	12.3	15.2
2	21.1	12.5	45.1	13	19.1
3	30.8	17.2	57	17	19.9
4	35	19.9	64.9	20	23
5	35.8	20.7	67	21.2	22.9
6	35.1	19.5	66.5	20.3	21.8
7	35.9	21	68	21.5	22.4
8	36.6	20	67.1	21.2	25.3
9	38.1	21.6	68.5	22.2	24.3
10	37.6	21.2	68.1	21.9	24.7
11	44.1	25.9	72.2	27.9	26
12	45	25.2	74.4	28.1	27.5
13	43.6	24.1	80.4	27.2	27
14	46.1	25.8	77	28	27.2
15	44	25.2	73.2	26	25.8
16	44.4	25.2	72.6	28	26.1
17	46.4	25.1	78	28.1	25.2
18	47.7	25.9	77	27.8	28.6
19	43.1	24.2	77.5	29	26.8
20	44.3	25	75.2	28.8	29.3
21	48.2	26.8	78.9	28.9	29.2
22	48.9	26	77.1	30	23.1
23	45	25.1	80.4	29.9	29.2
24	47.2	24.6	78.7	29.2	29.5
25	46.7	24.9	77.3	28.5	27.1
26	----------	25.9	79.9	28.3	28.8
27	49	26.1	80.9	28.9	26.8
28	47.1	26.9	83.6	29	27.8

TABLE 2.—*Measurements, in millimeters, and counts of individual specimens of* Auxis tapeinosoma *Bleeker*—Continued

Specimen No.	Length second dorsal base	Length anal base	Eye diameter	Maxillary length	First dorsal rays
1	7	6.1	6.6	11	10
2	8	8.7	7.5	11.8	10
3	9.1	10	9.1	14.1	10
4	10.4	10.3	10.5	16.4	11
5	10.5	10.4	10.2	16.2	10
6	11.7	10.4	11	16.1	10
7	9.5	10.1	10.8	16.3	10
8	10.7	10.6	10	16	10
9	12	11.2	10.1	16.3	10
10	11.9	11.7	10.1	16.5	10
11	15.1	13.2	12.4	19.2	10
12	12.2	11.7	12.1	19.1	10
13	11.1	11.9	12.1	19	10
14	11.1	11.8	12.7	20	10
15	12.5	11.1	12.7	19.2	10
16	13.3	11.3	12.6	19.7	10
17	12	12.5	12.8	19.9	10
18	13.1	12.2	12.6	19.2	10
19	11	11.2	12.4	19	10
20	13.9	13.8	12.1	20.4	10
21	12.7	11.2	12.4	20	10
22	10.3	12.2	12.8	20	9
23	12.9	13.6	13	20.4	10
24	12.5	13.5	12.1	20	10
25	12	11	12.3	19.8	10
26	12.2	12.1	13	20.7	10
27	12.9	11.9	12.2	19.9	10
28	12.9	12.2	12.8	20.1	10

Specimen No.	Second dorsal rays	Dorsal finlets	Anal fin rays	Anal finlets	Gill rakers
1	11	8	12	7	11+1+35
2	11	8	12	7	11+1+33
3	11	8	14	7	11+1+34
4	11	8	13	7	10+1+34
5	11	8	13	7	11+1+32
6	11	8	14	7	----------
7	11	8	13	7	11+1+33
8	11	8	14	7	11+1+33
9	11	8	12	7	10+1+34
10	11	8	13	7	----------
11	12	8	13	7	11+1+31
12	11	8	14	7	11+1+35
13	10	8	13	7	11+1+35
14	11	8	13	7	10+1+33
15	11	8	14	7	11+1+35
16	11	8	14	7	11+1+34
17	11	8	13	7	10+1+33
18	11	8	13	7	11+1+34
19	11	8	13	7	11+1+34
20	12	8	14	7	11+1+33
21	11	8	12	7	10+1+35
22	11	8	13	6	10+1+33
23	12	8	14	7	11+1+34
24	11	8	13	[1] 4	10+1+34
25	11	8	14	7	11+1+35
26	11	8	14	7	11+1+34
27	11	8	12	7	11+1+33
28	11	7	14	7	10+1+34

[1] Specimen not deformed; no indication of injury to this part.

Several external characters and one easily accessible internal structure serve to distinguish the two Philippine species, the most obvious of which is the length of the posterior prolongation of the corselet along the lateral line. In *Auxis thazard* the corselet tapers abruptly toward the lateral line, narrowing rapidly to a few irregular scale rows above and below the lateral line about half way between the first and second dorsals. The corselet is 2 to 4 irregular scale rows wide at a vertical through second dorsal. In large specimens (350 to 400 mm. standard length) the corselet tapers less rapidly than in small specimens, but in no case does it extend to below the origin of the second dorsal. In the field it may be difficult to determine the end of the taper of the corselet, especially if the fish is moist or covered with slime. Turning the fish so that the light is reflected at the proper angle or drying the side of the fish will, however, aid in revealing it.

In contrast to the abrupt tapering of the corselet in *Auxis thazard*, the corselet of *A. tapeinosoma* decreases gradually almost the entire length of the body, and ends slightly before or behind the second dorsal finlet. At a vertical through the origin of the second dorsal the corselet is 7 to 12 irregular scale rows wide. The difference between the corselets of the two species is easily seen after a few specimens of each have been examined.

Another character that can be used in the field to separate the two species is the roundness of the body and the general appearance of the fish. The body is almost perfectly rounded, fusiform, cigar-shaped in *Auxis tapeinosoma*, but in *Auxis thazard* the body is definitely compressed, the sides are flattened, not rounded as in *tapeinosoma*. After a few specimens have been handled the feel and appearance of the fish are useful in a rough sorting of the two species.

The total gill-raker count is an excellent means of separating these two forms. Only a slight overlap in count occurs between the species, and the length of the posterior extension of the corselet easily distinguishes the two forms when this occurs. The gill rakers of 161 specimens of *A. thazard* and 55 specimens of *A. tapeinosoma* were counted and in one specimen only did the total count of *A. tapeinosoma* fall within the upper limit of that of *A. thazard*. The total gill-raker count on the first gill arch of *A. thazard* varies from 37 to 43, and with one exception, *A. tapeinosoma* has a count of 44 to 47 (43 in one specimen). Table 3 gives the total gill-raker count on the first gill arch of the two species and table 4 the total count in its component parts.

The two species may be differentiated also by several minor taxonomic characters such as head length, depth, tip of snout to anal origin, and length of first to second dorsal origins. Table 5 is a summary of several proportional measurements between specimens of approximately the same length of the two species.

TABLE 3.—*Total gill-raker counts of* Auxis thazard *and* Auxis tapeinosoma

Total number of gill rakers	*Auxis thazard*	*Auxis tapeinosoma*
37	2	---
38	14	---
39	39	---
40	48	---
41	30	---
42	23	---
43	5	1
44	---	12
45	---	17
46	---	14
47	---	11
Total number of specimens examined	161	55

TABLE 4.—*Gill-raker counts of* Auxis thazard *and* Auxis tapeinosoma

Specimen	Upper arch				Center	Lower arch								
	8	9	10	11	1	27	28	29	30	31	32	33	34	35
A. thazard	2	70	88	1	161	3	26	53	46	26	5	---	---	---
A. tapeinosoma	---	2	24	29	55	---	---	---	---	---	2	15	26	12

	Upper arch and center gill raker	Lower arch								
		27	28	29	30	31	32	33	34	35
A. thazard	8+1	---	1	---	1	---	---	---	---	---
Do	9+1	1	15	27	22	5	2	---	---	---
Do	10+1	2	10	26	23	21	3	---	---	---
A. tapeinosoma	9+1	---	---	---	---	---	---	2	4	---
Do	10+1	---	---	---	---	---	---	9	9	---
Do	11+1	---	---	---	---	---	1	5	14	11

Juvenile Stages of the Genus *Auxis*

Juvenile forms of the genus *Auxis* have previously been recorded from other parts of the world, but until now nothing has been known of the juvenile forms from the western Pacific. In the Mediterranean, De Buen (1932), Sparta (1933), Sella (1924), and Ehrenbaum (1924) have reported the young of this genus, and Schaefer and Marr (1948) discovered and studied juvenile forms from the west coast of central America. During the course of the first year of field work, the biological staff of the Philippine Fishery Program collected 19 specimens of young

TABLE 5.—*Summary of counts and proportional measurements*[1] *of specimens of* Auxis thazard *and* Auxis tapeinosoma *of approximately equal length*

Item	*A. tapeinosoma* 186–190	*A. thazard* 182–186.4	*A. tapeinosoma* 192–199.1	*A. thazard* 196	*A. tapeinosoma* 122–129	*A. thazard* 118–123	*A. tapeinosoma* 161.9	*A. thazard* 154–156.7
Head	4.4–4.5	4.15–4.35	4.36–5.1	4.2	4.35–4.14	4.16–4.2	4.5	4.19–4.32
Snout to first dorsal	3.28–3.4	3.2–3.21	3.28–3.33	3.15	3.25–3.34	3.15–3.23	3.42	3.14–3.21
Snout to second dorsal	1.56–1.57	1.61–1.66	1.54–1.58	1.6	1.56–1.76	1.57–1.74	1.57	1.48–1.62
Snout to anal	1.44	1.47–1.48	1.42–1.44	1.34	1.45–1.56	1.48–1.51	1.44	1.50–1.54
Depth	5.3–5.31	5.26–5.45	5.14–5.35	4.55	6.05–6.1	4.9–5.3	5.24	4.9–4.95
Pectoral to first dorsal	9.2–9.95	9.5–10.1	9.08–9.42	9.3	10.3–11.5	9.45–10.1	9.38	8.6–8.85
Length first to second dorsal origin	2.8–2.88	3.2–3.24	2.83–2.93	3.15	2.86–2.98	3.12–3.18	2.83	3.2–3.25
Pectoral length	8.95–9.35	8.62–9	8.83–9.12	8.95	9.91–9.93	9.5–10.8	9.5	9.28–9.35
First dorsal base	6.68–8.54	6.15–6.8	7.60–8.6	7.02	6.75–8.1	4.92–7.15	8.1	6.0–6.85
Second dorsal base	15.9–18.1	14.9–16.6	16.3–20.2	19.2	16.2–17.6	15.6–19	17.2	14.6–18.4
Anal base	17.8–18.3	16.7–17.6	17–19	17.3	14.8–21.1	15.9–19.7	16.2	14.9–16.2
Eye	3.71–4.22	4.4–4.66	4.04–4.42	3.71	8.94–4.2	4.17–4.3	3.98	4.45–4.78
Maxillary	2.56–2.66	2.52–2.58	2.67–2.76	2	2.5–2.52	2.32–2.46	2.54	2.46–2.55
First dorsal	10–11	11–12	10	11	10	11	10	10–11
Second dorsal	11	11	11	11	11	10–11	11	10–11
Dorsal finlets	8	8	8	8	8	8	8	8
Anal	13–14	13–14	12–13–14	14	12	10–12–13	14	13–14
Anal finlets	7	7	7	7	7	7	7	7
Gill rakers	10+1+34	10+1+31	11+1+33	9+1+29	11+1+33	9+1+29	11+1+34	10+1+31
Do	11+1+32	8+1+30	11+1+33	----------	11+1+35	10+1+31	----------	10+1+30
Do	----------	----------	10+1+34	----------	----------	10+1+27	----------	----------

[1] All proportional measurements are expressed in millimeters and are into standard length, except the maxillary which is into head length.

Auxis. Four specimens were collected by night-light operations from the research vessel *Spencer F. Baird*, two by the experimental fishing vessel *Theodore N. Gill*, and thirteen were found in the public markets of Menado, Celebes, Dutch East Indies, and Batangas, Luzon, Republic of the Philippines.

Twelve of the preceding juvenile specimens, identified as *Auxis thazard*, were collected from the following localities: 3 specimens, 21.8 to 26 mm. standard length, Minis Island, Pilas Island Group, Sulu Archipelago, lat. 6°36′ N., long. 121°34.5′ E., night light, May 7, 1948, *Spencer F. Baird;* 1 specimen 43.5 mm. standard length, Marigabato Point,

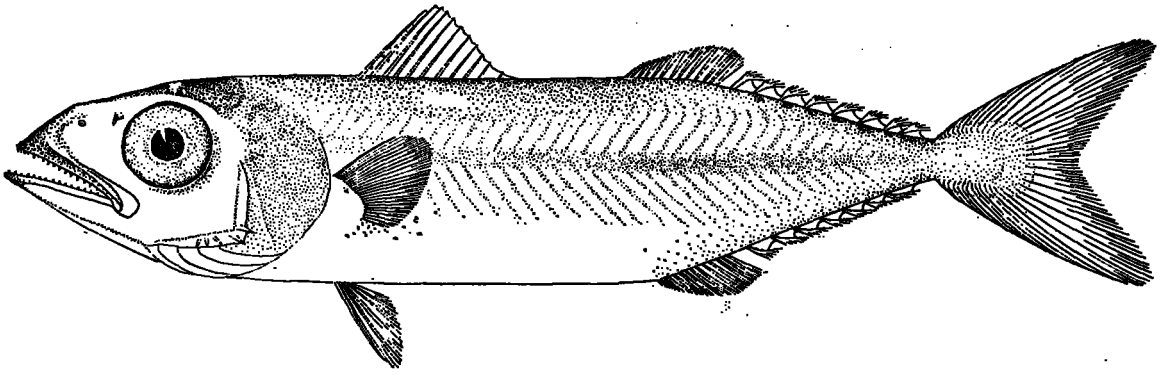

FIGURE 3.—Juvenile *Auxis thazard*, 23.1 mm. fork length.

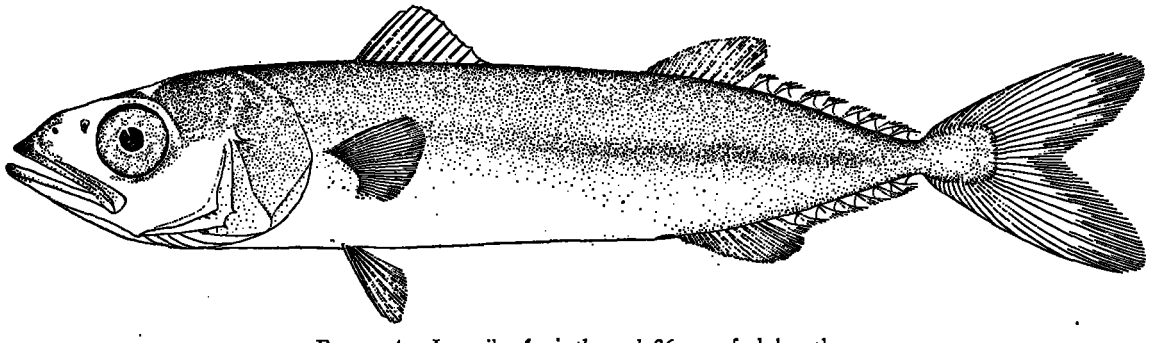

FIGURE 4.—Juvenile *Auxis thazard*, 26 mm. fork length.

southern Mindanao Island, lat. 7°21′ N., long. 124°12′ E., May 11, 1948, night light, *Spencer F. Baird;* 1 specimen 22.6 mm. standard length, Mouth of Sibuguey Bay, Mindanao Island, April 7, 1948, night light, *Theodore N. Gill;* and 7 specimens 45 to 55 mm. standard length, Batangas Public Market, Luzon, April 20 to 30, 1948.

Seven specimens of young *Auxis tapeinosoma* were captured at the following stations: 6 specimens 42 to 75.6 mm. standard length, Menado, Celebes, Dutch East Indies, March 6, 1948, night light, *Spencer F. Baird*, and market collections; 1 specimen 32 mm. standard length, Lamhil Island, near Basilan Island, Zamboanga, Mindanao, April 15, 1948, night light, *Theodore N. Gill.*

Extensive night-light operations carried out under a wide variety of conditions and localities have revealed but relatively few young tuna or tuna-like fishes. Those taken were collected during the first half of May 1948. Both over-water and submerged lights were tested, but for attracting the larger macroplankton and larval fishes it is believed that the under-water light is more satisfactory. A light suspended above the surface of the water seems to be more attractive to the larger fishes. Two lights are used at each station and one or two men operate fine-meshed dipnets at each light. The dipnet bags are made from nylon mosquito netting, which has been found to be durable material under tropical conditions of humidity and heat. The operators constantly dip from the collection of animal life surrounding the light, and after several dips the catch is placed in a pail of seawater and the process repeated. The catch thus brought aboard is closely examined for the young pelagic fishes. An adequate sample from the night light collection is preserved and returned to the shore laboratory for additional study.

Careful study of the juvenile *Auxis* in the collection shows that, as in the case of the adults, they can be separated into two species on the basis of gill-raker counts. These counts are tabulated in tables 6 and 7. The gill rakers correspond to the adults of the two species found in these waters, *A. thazard* and *A. tapeinosoma*. All gill-raker counts were made under 45 to 60 diameter magnification with a wide-field binocular microscope and every nodule indicating the development of a gill raker was tabulated. No doubt some errors may have been made in the gill-raker count of very small specimens, but no difficulty should be experienced in specimens 25 to 30 mm. standard length.

TABLE 6.—*Standard length and gill-raker count of juvenile* Auxis thazard

Standard length (millimeters)	Gill-raker count
21.8	[1] 4+1+18=23
22.6	10+1+30=41
26	7+1+29=37
26	10+1+31=42
43.5	10+1+29=40
44	8+1+29=38
46	8+1+30=39
47	9+1+29=39
47	9+1+29=39
48	9+1+29=39
49	8+1+30=39
55	9+1+29=39

[1] Lesser count possibly is due to the small size of the specimen with undeveloped gill rakers.

Two exceptions to the usual range of gill-raker counts were noted. One juvenile form, with a standard length of 21.8 mm., had a gill-raker count of 4+1+18 for a total of 23 gill rakers. The second example, from an adult fish, had a count of 8+1+22 for a total of 31 gill rakers. It is possible that the gill rakers were not fully developed in the juvenile specimen, or that the gill arch was deformed or injured in some manner to cause this abnormal count. On the other hand, no difficulty was experienced in

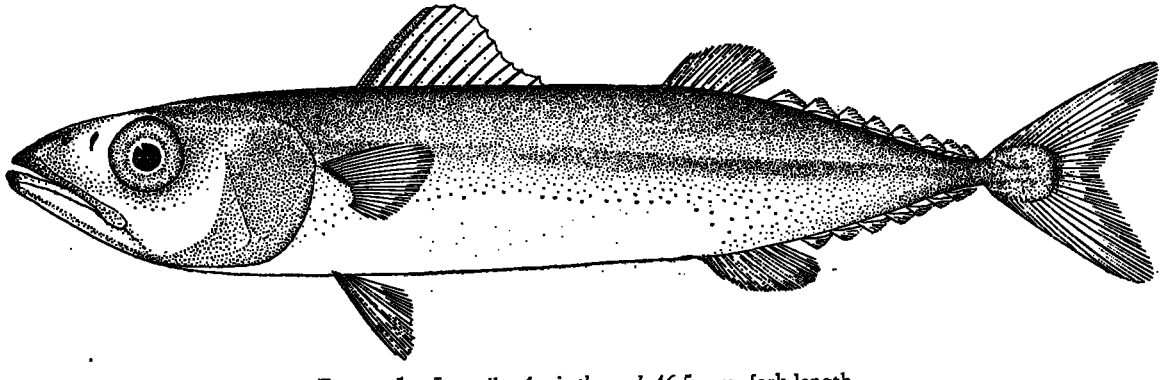

FIGURE 5.—Juvenile *Auxis thazard*, 46.5 mm. fork length.

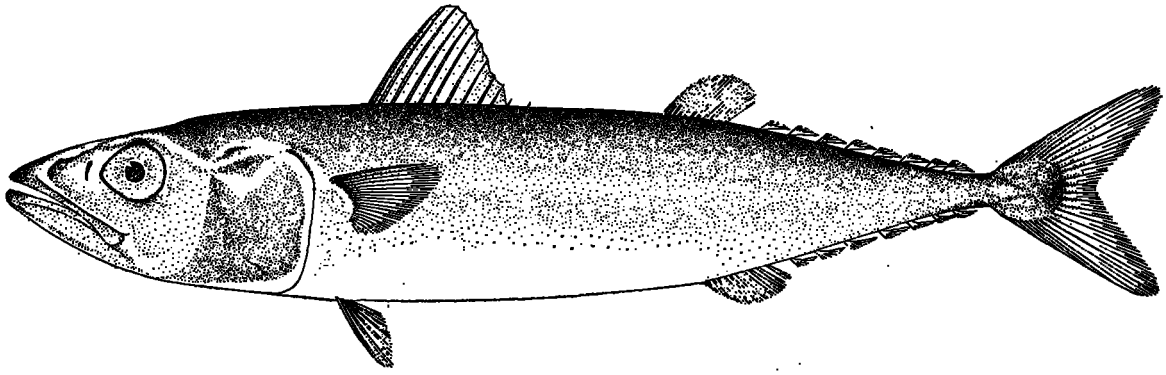

FIGURE 6.—Juvenile *Auxis thazard*, 57.2 mm. fork length.

counting the gill rakers of specimens of similar size and there was no indication of abnormality or injury to the gill arch. The large gill arch from a mature specimen was found in a collection of adult *Auxis* gill rakers made at Batangas, Luzon. Examination of this gill arch showed that it appeared normal in every way. Unfortunately, the specimen was not preserved and is unavailable for study. Since one of the two fundamental differences between the two species of Philippine *Auxis* is the difference in the gill-raker counts, it is possible that a third species may be present in the islands, although extremely rare.

Juvenile *Auxis* can be distinguished from the young of *Neothunnus* and *Euthynnus*, commonly found in Philippine waters, by the wide interspace between the first and second dorsal fins and the absence of a wholly or partly black first dorsal. From *Katsuwonus*, another genus of the same family, young *Auxis* can be distinguished by the wide interspace between the fins. In coloration the first dorsal of *Auxis* and *Katsuwonus* are somewhat similar both having a lightly pigmented or colorless fin. Although light in color, the first dorsal of *Katsuwonus* possesses more pigment than that of *Auxis*. Distally the first dorsal of *Katsuwonus* is more or less light brown or tan in color, while in *Auxis* the color is confined to a few scattered chromatophores along several of the anterior rays.

The young of two genera of the family Scombridae, possibly, can be also confused with young *Auxis*. These genera, *Rastrelliger* and *Pneumatophorus*, while possessing the wide interspace between the dorsal fins, have only 5 dorsal and anal finlets in contrast to 8 dorsal and 7 anal finlets of *Auxis*. Although there is little chance of confusing juvenile *Auxis* with the remaining two genera of Scombroid fishes found in the Philippines, *Acanthocybium* and *Scomberomorus*, it is well to point out that each of these two genera possess 9 dorsal and anal finlets, and the interspace between the two dorsal fins is greatly reduced.

Except for the fact that the small specimen (32 mm. standard length) of *Auxis tapeinosoma* has its full complement of gill rakers, one would suppose that the larger juvenile specimens of *Auxis thazard* were the same species with the gill rakers not fully

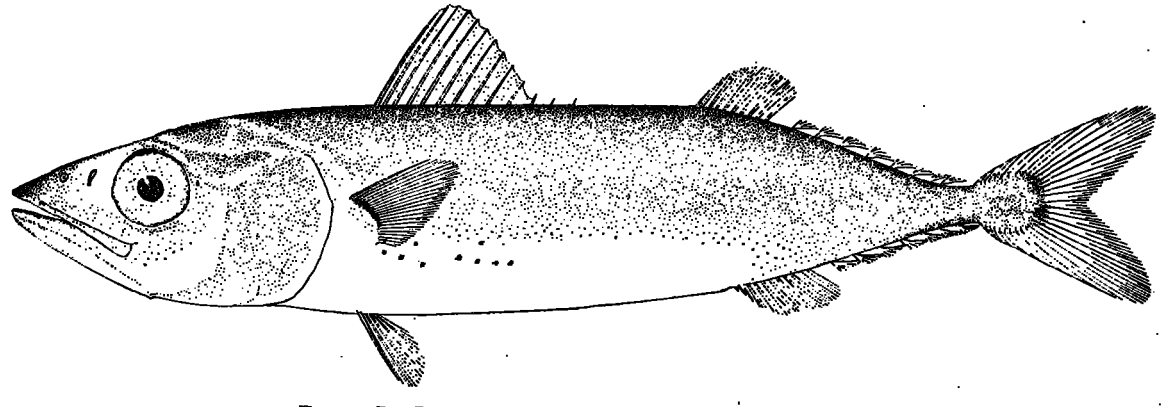

FIGURE 7.—Juvenile *Auxis tapeinosoma*, 33 mm. fork length.

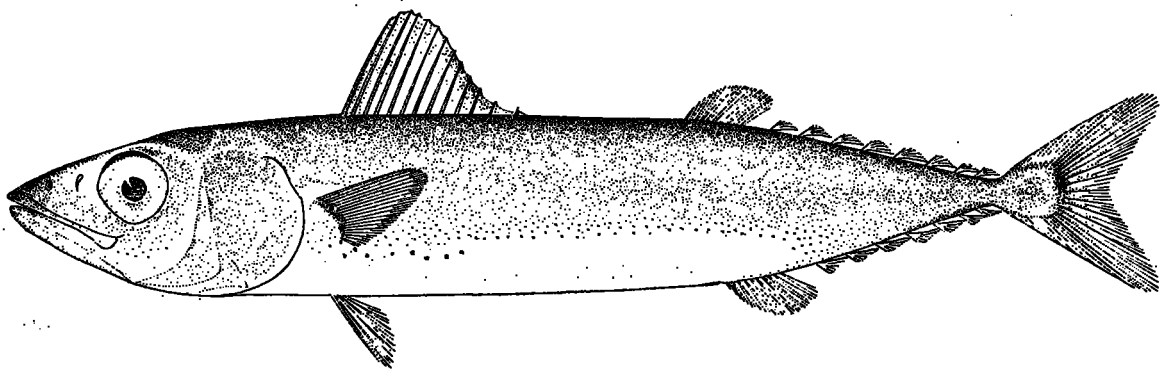

FIGURE 8.—Juvenile *Auxis tapeinosoma*, 44 mm. fork length.

developed. Counts made on both species (tables 6 and 7) show that this cannot be so, for the two counts widely overlap in the standard lengths of the two species. On the basis of present knowledge, it would seem that the supposition of Schafer and Marr (1948) is correct, that possibly they had the juvenile forms of two species. They list two specimens (52 and 54 mm. total length) with a total gill-raker count of 48 and 46, well within the limits of the total count for that of *tapeinosoma*. They also recorded total gill-raker counts of 39, 41, and 42 for specimens 42, 48, and 68 mm. in total lnegth, which fall within the limits of those for *Auxis thazard*, as here defined. Schaefer and Marr also refer to two adult specimens of *Auxis* from Culion, Republic of the Philippines, and from the gill-raker counts, it is possible that they also belong to two species. The specimen with the gill-raker count of 12+35=47 is most likely *A. tapeinosoma*, and the second specimen with a count of 11+32=43 gill rakers seems to be *A. thazard* as classified in this paper.

TABLE 7.—*Standard length and gill-raker count of juvenile* Auxis tapeinosoma

Standard length (millimeters)	Gill-raker count
32	10+1+35=46
42	11+1+34=46
48	10+1+34=45
51.5	10+1+35=46
58.5	10+1+34=45
61	10+1+34=45
75	10+1+36=47

The color pattern of the young of both species is essentially the same, although in specimens of equal size *tapeinosoma* is slightly darker in color and the pattern more widely distributed. In the smaller specimens of both species the most pronounced areas of pigmentation are on the upper jaw, tip of lower jaw, tip of snout, around the posterior-ventral margin of the eye, the operculum, dorsally on head between the eyes, dorsally along midline of back, along midline of sides, along base of anal fin, and around base of urostyle. Large chromatophores in the peritoneum are visible through the thin body wall especially behind and below the base of the pectoral fin. The pigmentation of the first dorsal fin is slightly more in *Auxis tapeinosoma* than in *thazard*. In the latter species the first dorsal is colorless except for a slight pigmentation along the edge of the anterior rays, while in the former the anterior interspinous membranes are lightly pigmented, especially distally. As the two species increase in size the localized areas of pigmentation gradually spread until finally the color reaches the midline of the sides anteriorly and to the anal base posteriorly. A faint longitudinal dark band extends along midline of sides, bordered above and below by slightly less pigmented areas. The head also becomes progressively more pigmented as the fish increases in size. The fins remain unpigmented except the first dorsal which becomes lightly tinged with brown especially distally on the posterior interradial membranes in *thazard*, and similar but darker in *tapeinosoma*.

In the smaller specimens the dorsal and ventral outlines are distinctly angulated. Both outlines are flat and almost parallel to one another from the posterior part of the head to beneath the second dorsal fin. At this point the outlines bend abruptly toward the caudal region. The dorsal outline of the snout is distinctly angular. Both the dorsal and ventral outline become more broadly and evenly rounded as the fish increase in size.

Preopercular spines are present on the fish up to, at least, 30 mm. standard length. On one small

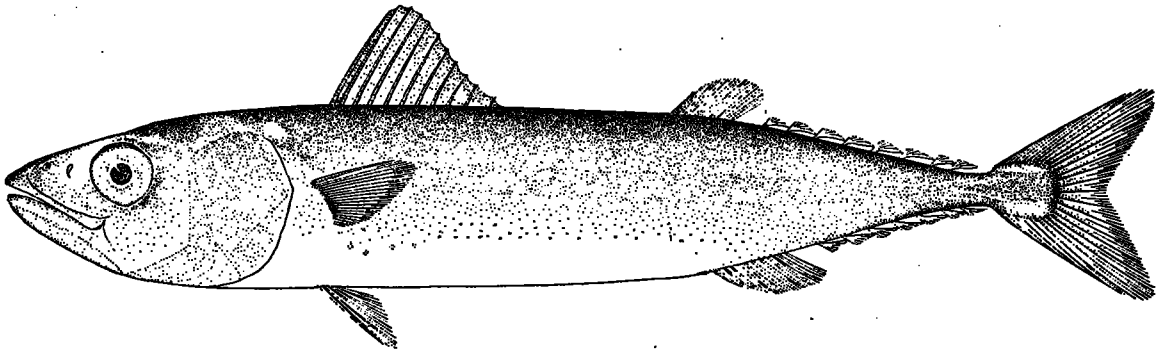

FIGURE 9.—Juvenile *Auxis tapeinosoma*, 54 mm. fork length.

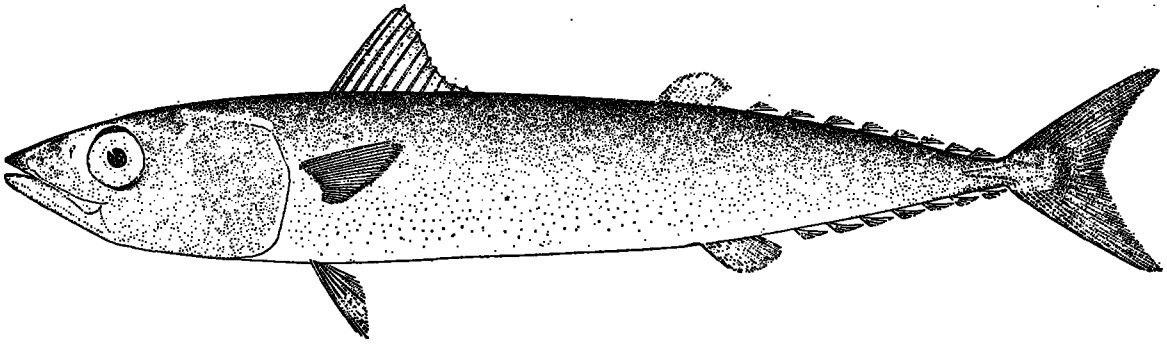

FIGURE 10.—Juvenile *Auxis tapeinosoma thazard*, 79 mm. fork length.

specimen of 21.3 mm. five spines are visible, but on a 25.6-mm. specimen only three spines were seen. In the larger specimens spines are not visible, being concealed in the tissue covering the preoperculum. Schaefer and Marr (1948) counted 9 preopercular spines in stained specimens.

A single row of small, conical, pointed teeth is present on each jaw. Philippine specimens are similar in this respect to those from the eastern Pacific with about 20 teeth on each side of the upper jaw, and about 25 on each side of the lower jaw. A few minute granulations are present on the palatines, but there is no evidence of teeth on the vomer of either species.

SUMMARY

The genus *Auxis* family Scombridae is a food fish of some importance in the Republic of the Philippines. Until recent investigations by biologists of the Philippine Fishery Program of the Fish and Wildlife Service, it was thought that the commercial catch was composed of only one species. It can now be shown that two species are present, *Auxis thazard* and *Auxis tapeinosoma*. The two species can be readily distinguished by the differences in gill-raker counts and the structure of the corselet. In *A. thazard* the total gill-raker count of the first gill arch is 37 to 43, and in *A. tapeinosoma* it is mostly 44 to 47 (43 in one of 55 specimens). The posterior prolongation of the corselet along the lateral line tapers abruptly in *thazard* and is only 2 to 4 scale rows wide below the origin of the second dorsal, while in *tapeinosoma* it tapers evenly and gradually throughout its length, being 7 to 12 irregular scale-rows wide under the origin of the second dorsal.

Juvenile forms of the genus *Auxis*, previously unknown from the Indo-Pacific region, have been collected and identified as to species. As with the adults, they can be separated into two species on the basis of gill-raker counts. These counts correspond to the adults of the two species found in Philippine waters, *A. thazard* and *tapeinosoma*. One juvenile and one adult specimen with lower gill-raker counts point to the possibility that perhaps a third species may be found, although it seems to be extremely rare. No attempt has been made to revise the confused systematic status of this genus, since neither adequate collections nor library are available for study. Rather, it is hoped that the data assembled here will aid future research on this genus.

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DEFINITIONS OF BODY DIMENSIONS USED IN DESCRIBING TUNAS

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DEFINITIONS OF BODY DIMENSIONS USED IN DESCRIBING TUNAS

Opportunities have recently been afforded us to collect biological data on several species of tunas in various regions of the Pacific Ocean. The problem of whether there exists in each species one or more populations has been of major interest. It is important to know for any commercially utilized species, and especially for pelagic species of wide distribution such as the tunas, whether exploitation at any point in their range bears upon the whole stock, or whether exploitation at one point will not affect the stock at another point. The classical method of distinguishing subpopulations in systematic and fisheries work is that of comparing series of meristic counts and morphometric characteristics among samples taken at different localities throughout the range of the species. Due to the improbability of one or two individuals being able to examine an adequate series of tunas over a broad area within a reasonable period of time, our data are being made available as soon as possible, so they may be used by other workers. One such report has already appeared (Schaefer 1948). In order to facilitate the use of our data, the methods used are defined here. Many of them have been given by Godsil and Byers (1944), but some have been modified by Schaefer (1948), and additional ones will be used later. It seems worth while that, for convenience, they be set forth in one place.

Originally, a comprehensive list of meristic and morphometric characters was drawn up, but field experience demonstrated the unwieldiness of such an extensive list. The characters used were selected (1) with a view to choosing those that would be likely to show possible differences; (2) because of facility in counting or measuring; and (3) because of their use by previous workers. There is, of course, no assurance that these particular characters will be of value in identifying discrete populations, if such exist. In all probability the list will have to be modified and expanded from time to time.

In collecting our data, an effort has been made to examine fish in the entire size range available at any one locality. This permits the various body proportions to be expressed as the regression of one dimension on another, such as the regression of head length on total length. The necessity for the comparison of regressions rather than ratios arises from the fact that the different parts of the body grow at different rates, as has been shown for *Neothunnus macropterus* by Schaefer (1948) and for *Thunnus thynnus* of the Atlantic by Frade (1931a). Most of the morphometric data on tunas both from the Atlantic-Mediterranean region (Anon. 1933; Frade 1929, 1931a, 1931b; Heldt 1928, 1931) and from the Pacific (Godsil and Byers 1944) have been in the form of ratios of one dimension to another. These data are of small value for comparing the fish from one region with those of another, because of the differential growth rate of different parts of the body. It is important that researchers in different parts of the world publish either the original measurements or the statistics describing the regressions with the ranges of size to which they apply, or, preferably, both.

The specimens examined by us were all fresh-caught. It is desirable that measurements of fresh-caught fish form the basis of comparisons until such time as the effects of freezing or chemical preservation on the body proportions have been determined to have constant effects and those effects are firmly established. The natural variability of most dimensions is relatively small (Schaefer 1948) so that the effect of preservation on differential shrinkage or expansion of different body parts might lead to spurious results if samples of preserved fish from one region were compared with samples of fresh fish from another, or if samples of fish from two different regions had undergone different preservative treatment. Of course, this does not apply where countable characters rather than measurements are concerned.

The measurements described are all made in metric units with calipers (of the type mentioned by Godsil and Byers 1944) or dividers, depending upon the size of the fish and the distance to be measured. All distances are straight line. The tip of the fixed arm of the calipers (or one point of the dividers) is applied to the first point mentioned and the tip of the sliding arm of the calipers (or the other point of the dividers)

is applied to the second point mentioned. Where a choice of sides is involved, all measurements and counts are made on the left side of the fish.

Total length.—The distance from the tip of the snout (most anterior point on upper jaw), with jaws closed, to the cartilaginous median part of the caudal fork (seating the sliding arm of the caliper firmly and thus depressing the small fleshy flap extending posteriorly).

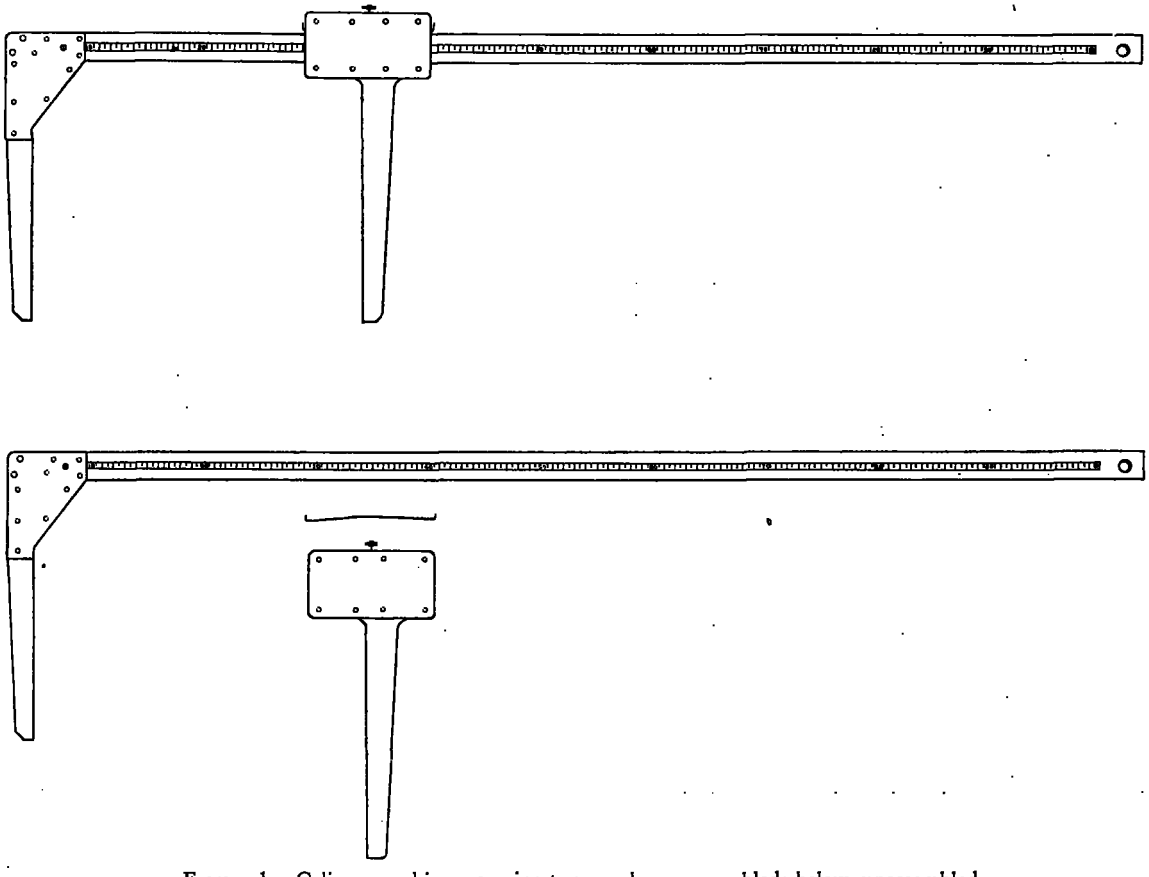

FIGURE 1.—Calipers used in measuring tunas; above, assembled; below, unassembled.

Head length.—The distance from the tip of the snout to the most posterior point on the margin of the subopercle (depressing the fleshy flap extending posteriorly).

Snout to insertion first dorsal.—The distance from the tip of the snout to the insertion of the first dorsal. The insertion of the first dorsal is the intersection of the anterior margin of the first dorsal spine, when the fin is held erect, with the contour of the back. This point is identical with the most anterior point of the first dorsal fin slot.

Snout to insertion second dorsal.—The distance from the tip of the snout to insertion of the second dorsal. The insertion of the second dorsal is not so clearly defined as the insertion of the first dorsal, particularly on larger fish, but is the intersection of the anterior margin of the second dorsal, when the fin is held erect, with the contour of the back. When the second dorsal is raised, the determined point should be marked with thumbnail or scalpel.

Snout to insertion anal.—The distance from the tip of the snout to the insertion of the anal. The insertion of the anal is determined in the same manner as the insertion of the second dorsal.

Snout to insertion ventral.—The distance from the tip of the snout to the insertion of the ventral. The insertion of the ventral is the intersection of the anterior margin of the ventral, when the fin is extended, with the contour of the body.

Greatest depth.—The greatest vertical distance between the dorsal and ventral contours. The measurement is taken from the dorsal body contour to the ventral body contour, with the first dorsal fin depressed in its slot. It is oriented by reference to

the dorsal spine, the insertion of which is at or nearest the upper end of the vertical. Dorsal spines are counted posteriorly, the most anterior spine being the first.

Length pectoral.—The distance from the insertion of the pectoral to the most posterior point, taken with the pectoral fin extended posteriorly and opposed to the side. The insertion of the pectoral is the intersection of its dorsal margin with the body.

Pectoral insertion to insertion first dorsal.—The distance from the insertion of the pectoral fin to the insertion of the first dorsal.

Length base first dorsal.—The distance from the insertion of the first dorsal to the insertion of the second dorsal.

Length base second dorsal.—The distance from the insertion of the second dorsal to the intersection of the posterior margin of the second dorsal with the contour of the back. Note that this includes any finlet that is attached to the second dorsal. Because of the difficulty in determining whether or not a finlet is "attached" (i. e., contiguous with the second dorsal) it is not a very good character.

Spread caudal.—The distance between the dorso-posterior extremity of the caudal and the ventro-posterior extremity of the caudal. This measurement is accurate only if the caudal extremities are not frayed, the fish has not been handled extensively by the tail, and the fish has not been out of the water long enough for the caudal to dry (and possibly shrink).

Length longest dorsal spine.—The distance from the insertion of the longest spine to its distal end. The insertion of the spine, with the fin held erect, is the intersection of its anterior margin with the contour of the back.

Length first dorsal spine.—The distance from the insertion of the first dorsal spine to its distal end.

Length second dorsal.—The distance from the insertion of the second dorsal to its distal end, with the fin in a normal position. Note that this fin is often extended in a long filament, especially in large *Neothunnus*, and care should be taken to notice if this extension is frayed.

Length anal.—The distance from the insertion of the anal fin to its distal end, with the fin in a normal position. Remarks under "length second dorsal" apply here.

Length longest dorsal finlet.—The distance from the insertion of the longest dorsal finlet to the end of its posterior filament. The insertion of the finlet is the intersection of its anterior margin with the contour of the body. Dorsal finlets are identified by number. They are numbered anteriorly, the most posterior one being the first.

Diameter of iris.—The greatest diameter measured to the margin of the yellow iris and the adjoining black tissue. This is generally not on a line parallel to the median line of the body.

Length maxillary.—The distance from the tip of the snout to the posterior end of the maxillary.

Least depth caudal peduncle.—The least vertical distance between the dorsal and ventral contours of the caudal peduncle.

Greatest width caudal peduncle at keels.—The greatest horizontal distance between the lateral contours including the keels. Note that the keels may be broken or shrunken (due to drying).

Number of first dorsal spines.—The total number of spines discernible with the first dorsal held erect and with no dissection. The most posterior spine may be completely subcutaneous and is then not counted.

Number of dorsal finlets.—The number of finlets following the second dorsal. The most posterior one is counted as the first, and finlets attached to the second dorsal are counted separately. For example, 9=9 free finlets; 8+1=8 free finlets plus 1 finlet attached to the second dorsal. It is often difficult to decide whether or not a finlet is attached, and consequently this character may be of little use.

Number of anal finlets.—The number of finlets following the anal fin. Counted in the same manner as the dorsal finlets.

Number of gill rakers.—The number of anterior rakers on the most anterior gill arch on the left side of the fish (some species also have posterior rakers on this same arch). The counts of the rakers on the two arms of the arch are kept separate. For example, 10+20=30 gill rakers with 10 on the upper arm and 20 on the lower. The counts include all rakers that can be seen or felt with a dissecting needle. We have encountered no difficulty in assigning rakers near the angle of the arch to one arm or the other.

Sex.—Determined by inspection. Very immature males and females may be difficult to distinguish. Ovaries, which are tubular, may often roll between the fingers, while testes, which are solid, will turn over. The testes of ripening or ripe males are

enlarged, solid, white bodies, not round in cross section. The ovaries of ripening or ripe females are enlarged, turgid, pink or yellow-orange bodies, round in cross section. Ova may often be distinguishable with the naked eye. The testes of spawned-out males are less turgid, tougher, and pinker than those not spawned, and are difficult or impossible to distinguish from maturing testes in early stages. The ovaries of spawned-out females are hollow, more or less flabby, sac-like tubes.

Weight.—This has been determined in pounds on spring balances. Metric units would be more desirable, and experience has shown that a counterpoise style of balance, such as Chatillon No. 160, is more satisfactory, since the calibration of a spring balance is subject to change due to corrosion.

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OBSERVATIONS ON JUVENILE OCEANIC SKIPJACK (*KATSUWONUS PELAMIS*) FROM HAWAIIAN WATERS AND SIERRA MACKEREL (*SCOMBEROMORUS SIERRA*) FROM THE EASTERN PACIFIC

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UNITED STATES DEPARTMENT OF THE INTERIOR, J. A. Krug, *Secretary*
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From January to October 1948, the Pacific Exploration Co. operated the motor vessels, *Alaska* and *Oregon*, in exploratory tuna fishing in the waters around and southwest of the Hawaiian Islands. Scientists from the United States Fish and Wildlife Service were aboard these vessels to observe fishing activities and to collect biological and oceanographical data. I was aboard the *Oregon* from July through September 1948.

While operating in Hawaiian waters, seven juvenile *Katsuwonus pelamis* (Linnaeus) 1758 were collected. Six specimens, 113 to 118 mm. in total length,[1] were taken on July 13, from southwest of Oahu near 20°30′ N. latitude, 158°45′ W. longitude, and one specimen, approximately 183 mm. total length, was taken on September 3 off the Kona coast at 19°33′ N., 156°00′ W. The six small specimens were regurgitated by adult *K. pelamis*. The large specimen was removed from the stomach of an adult *K. pelamis*. These were preserved in formaldehyde and later transferred to a 70-percent alcohol solution. All specimens are somewhat damaged by digestion; however, they are easily recognized as scombroids by the body contours and the shape of the head. One specimen, 113 mm. in length, is in better condition than the remaining ones and is depicted in figure 1. The left side is undamaged except for a small area just ventral to the first dorsal fin. The following description is based mainly upon this fish.

Katsuwonus pelamis (Linnaeus) 1758

The belly is unpigmented except for a faint yellowish streak just posterior to the base of the ventral fins. There are no indications of lateral stripes. Pigmentation is concentrated at the level of the pectoral fin, and the whole dorsal surface above the level of the pectoral fin is darkly pigmented. Pigmentation extends beyond and below the caudal peduncle to the base of the caudal rays. The snout, upper and lower jaws, and the head anterior of the nape, are darkly pigmented subcutaneously. The upper posterior portion of the operculum is lightly pigmented. The most anterior dorsal spine is pigmented except at the distal end. There is a row of black spots along the posterior edge of this spine. Pigment is concentrated in the lower two-thirds of the second and third spines and at the base in the fourth and fifth spines. Coloration is lacking in the remainder of the visible spines. The first six rays of the second dorsal bear pigment spots extending about two-thirds of their length. Pigmentation of the dorsal fins differs from the 21-and 44-mm. specimens of *K. pelamis* from Central America, described by Schaefer and Marr (1948), in that in their specimens pigmentation is present in the distal half of the first dorsal and absent in the second dorsal.

A remnant of the corselet is present; presumably, the remainder was disgested. The anterior part of the lateral line is present and curves slightly upward over the pectoral. On the left side, the caudal peduncle has a lateral keel and a small dorsal and ventral keel at the base of the caudal. The right side is digested. The first dorsal has 14 visible spines with the second spine the longest. Space is present for two or three additional spines. Figure 1 is drawn with the two posterior spines reconstructed. Eight dorsal and seven anal finlets are present.

The intestine is straight except for one fold anterior to its origin. This fold is closely applied to the caecal mass. The caecal mass is large and extends the length of the body cavity. The liver is typical of the Katsuwonidae in that its right lobe is slender (Kishinouye 1923). This refers to the lobe on the specimen's right when the observer is looking at the dorsal surface and toward the fish's head. This lobe would be on the left when viewed ventrally, as reported by Schaefer and Marr (op. cit: 194).

The gill arches of this specimen show adult

[1] All lengths in this paper are the distance from the tip of the snout to the tip of the shortest median caudal ray.

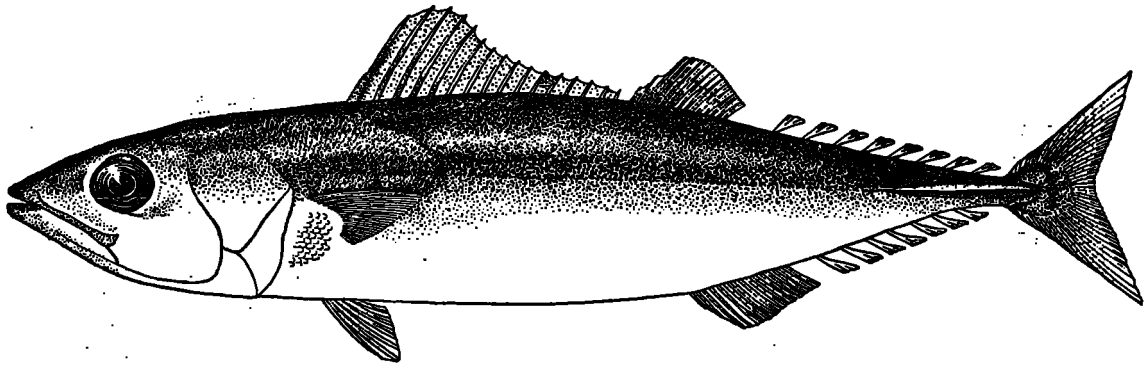

FIGURE 1.—*Katsuwonus pelamis*, 113 mm. long.

characteristics in the shape of the arch and fineness of the gill rakers. There are 16 gill rakers on the upper limb and 40 on the lower.

Four specimens were X-rayed for vertebral counts.[2] In addition, one specimen, approximately 116 mm. in length, was cleared and stained with alizarin dye after the method described by Hollister (1934). The vertebrae in the four X-rayed specimens each total 41 including the urostyle. It was not possible to determine the number of caudal and precaudal vertebrae from the X-ray plates. In the cleared and stained specimen there are 20 precaudal vertebrae. The tail region of this specimen is partially missing so it is not possible to make a total vertebral count. The structure of the vertebral column resembles the description given by Schaefer and Marr (op. cit: 194) of a *K. pelamis* 44 mm. in length, in that the "inferior foramina are large and well developed in precaudal vertebrae 14–20, as well as on the anterior caudal vertebrae." The "complex basket work," mentioned by Godsil and Byers (1944: 42), which is formed from the inferior foramina and haemal arches, is evident.

The characteristics of the vertebral column are sufficient to place these specimens in the Katsuwonidae of Kishinouye. Of the Katsuwonidae, the only species having a total of 41 vertebrae is *K. pelamis*. In addition, these specimens may be further separated from *Euthynnus* by the high gill-raker count. Therefore, classification as *K. pelamis* may be considered definite.

The discovery of these juvenile specimens indicates that *K. pelamis* spawns in the Hawaiian area. Although no juveniles have been previously reported from this area, Hawaiian commercial fishermen state that they have taken oceanic skipjack approximately 300 mm. in length. The discovery of juveniles and observations on maturity of adults has established a spawning area of oceanic skipjack off Central America (Schaefer and Marr 1948). Similar observations and collection of juveniles have established a spawning area in the Marshall Islands (Marr 1948). A paper by Kishinouye (1927) contains a description of a young oceanic skipjack 26 mm. in total length, taken from the stomach of an adult oceanic skipjack on April 14, 1924 near Suwase Jima (28°20′ N., 129° E.). Young fish, 3 to 6 mm. in total length, supposedly skipjack, are also noted. As this paper is not generally available, a translation is included here.[3]

Skipjack (Katsuwonidae): Larvae thought to be those of skipjack, two measuring approximately three millimeters in length, three of approximately four millimeters, and one specimen measuring almost six millimeters without the caudal fin, were recovered from plankton collections made by the Shoyo Maru off Shichito from late May to early June 1924. On the basis of comparisons with juveniles positively known to be skipjack, it is not thought unreasonable to conclude that these specimens are larval skipjack.

Larvae measuring approximately 3 millimeters in length were found among plankton collected southeast of Akuishijima on June 12, 1924. Having hatched only recently, they had just completed absorption of the yolk sac. Numerous melanophores are present about the brain, opercle, and body walls. The anterior body cavity narrows behind the head. The anus opens anterior of the tip of the pectoral fin. Teeth and opercular spines are not yet developed.

The larvae of approximately 4 millimeters in length were captured off Shichito during the summer of 1924. The head is well-developed; large sharp teeth, ten on both right and left sides, are present on the lower and upper jaws. Palatine teeth are absent as yet. Although myotomes are not well-formed posteriorly and their number difficult to determine, it appears as though 41 myotomes are present.

The head of the specimen which measures almost 6 millimeters

[2] These specimens and the *Scomberomorus maculatus* mentioned later were X-rayed through the courtesy of Dr. Dorothy J. Starks of Palo Alto, Calif.

[3] The reference to this paper was provided by Dr. Sidney Shapiro, and the translation was furnished through the courtesy of Bell Shimada, fishery research biologists, Pacific Oceanic Fishery Investigations, U. S. Fish and Wildlife Service.

without the caudal fin is large, and is nearly one-half of the body length. Both, eyes and mouth, are large, the tip of the snout is pointed and the upper jaw protrudes slightly beyond the lower jaw as in the specimens previously described.

Among my research material, the smallest specimen which can be clearly identified as a skipjack measures 26 millimeters in total length and was recovered by Mr. Umemoto on April 14, 1924 from the stomach of a skipjack taken at Gonsone. With the increase in width of the trunk so that it nearly equals the width of the head, the length has also increased; the anus has retreated posteriorly and opens immediately anterior to the anal fin. The fin (TN: no mention of any particular fin) is in line with the central axis of the body and the unpaired fins have also undergone specialization and resemble in form, those of the adults. The opercular spines have degenerated and are no longer conspicuous. The stomach is pointed and having become an elongated sac, occupies nearly the whole length of the body cavity. Pyloric caecae have developed on both anterior and posterior sides of the duodenum. Furthermore, by the presence of a pore in the urohyal there is no doubt that the specimen is the postlarva of a skipjack.

I have been unable to find any other reference to the presence of a pore in the urohyal of the Katsuwonidae. Examination of the urohyal in the specimens at hand revealed this bone to be very thin with a thick ridge at its ventral margin. It is translucent just above the ventral margin. Godsil and Byers (1944:45) noted this same characteristic. As Kishinouye's specimen was in a post-larval stage it is not unlikely that the urohyal was incompletely formed or that the area just above the ventral margin was transparent, thus giving the appearance of a pore.

Scomberomorus sierra (Jordan and Starks) 1895

The sierra mackerel is an excellent food fish found on the Pacific coast of Mexico and Central America. It is taken frequently by sportsmen and is probably abundant enough to support a sizable commercial fishery. However, this species has not been exploited to any degree. According to the California Division of Fish and Game (1935–47) the yearly deliveries to southern California from 1930–47 averaged slightly more than 13,500 pounds. The Atlantic cognate species (*Scomberomorus maculatus*) (Mitchill) 1815, is more extensively exploited. Landings along the South Atlantic States and Gulf States totaled 6,443,200 pounds in 1940 (Anderson and Power 1943). With the present world shortage of animal proteins, it is likely that a more important sierra-mackerel fishery will develop.

Little is known about the biology of the sierra mackerel. It is known to occur from Santa Monica south to the Galapagos Islands and Peru. Walford (1937:25) stated that fish taken in Mexico at the end of March had ripening ovaries and surmised that the spawning season was probably in late spring or summer. The capture of juveniles, which are probably *S. sierra*, tends to confirm this period and also indicates that spawning may take place earlier, perhaps during January or February in more southern waters. Limited spawning of *S. maculatus* has been reported off North Carolina from the latter part of June to nearly the end of August. (Hildebrand and Cable 1938:510). Earll (1882:404) had earlier reported that *S. maculatus* spawned in the Carolinas in April, in Chesapeake Bay in June, and in the vicinity of Long Island during late August to the middle of September.

The sierra mackerel is closely related to the Atlantic spanish mackerel (*S. maculatus*), if not identical with it. (Meek and Hildebrand 1923:325; Walford, 1937:24). The present description is intended to aid in correctly identifying these species when a more complete series of specimens is available.[4]

The following description is based on 12 juveniles ranging from 21 to 71 mm. in length. Eight specimens, 26.5 to 71 mm., were collected on March 24, 1939, from Potrero Grande Bay, Costa Rica, at 10°50′45″ N., 85°48′45″ W.[5] One specimen, 50.5 mm., was collected off Costa Rica (probably in the Gulf of Nicoya) in February 1947.[6] One specimen, 21.5 mm., was collected on September 24, 1948,and two specimens, 21 and 23.25 mm., were collected on September 25 from Ballenas Bay, Baja, Calif., at 26°43′ N., 113°30′ W.[7] All specimens were caught with dip nets at night, under flood lights and were preserved in formaldehyde. They were later transferred to alcohol. Two specimens, 43 and 61 mm., were cleared and stained for a study of skeletal structures. Representative specimens, 21 and 71 mm. total length, are depicted in figures 2 and 3.

As illustrated in figure 2, pigmentation in the smaller specimens is concentrated along the midline, along the bases of the dorsal and anal fins and finlets, on the nape, on the tip of the snout, and on the lower jaw. The brain covering is pigmented subcutaneously. The lateral peritoneum contains conspicuous melanophores. The posterior portion of the opercle contains melanophores, but is not so

[4] The name *Scomberomorus* (Lacépède) 1802, as opposed to *Cybium* (Cuvier) 1829, is used here following the discussion presented by Munro (1943: p. 66).

[5] Furnished through the courtesy of Dr. Rolf L. Bolin, Hopkins Marine Station, Stanford University.

[6] Furnished through the courtesy of M. B. Schaefer, Pacific Oceanic Fishery Investigations, U. S. Fish and Wildlife Service.

[7] Furnished through the courtesy of J. L. McHugh, Scripps Institution of Oceanography.

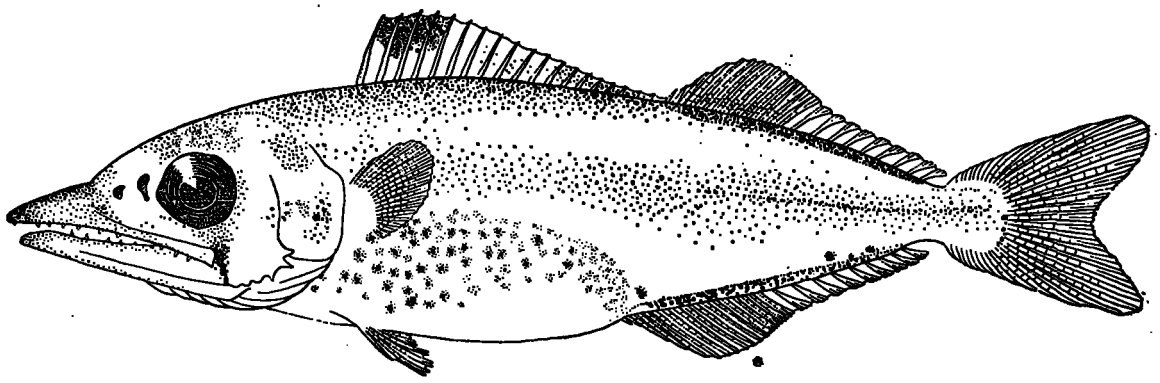

FIGURE 2.—*Scomberomorus sierra*, 21 mm. long.

darkly colored as the peritoneum. The distal half of the first dorsal is pigmented between the first and fifth spines and scattered spots are present along the length of the fin. The 21-mm. fish illustrated in figure 2 has a row of spots slightly above the base of the second dorsal fin. A similar, but lighter colored, row of spots is present just beneath the base of the anal fin. This coloration is not present in my other specimens although the base of the second dorsal is pigmented in fish larger than 39 mm. in total length. The remaining fins are colorless. At a total length of 26.5 mm. the snout and lower jaw are darker. The concentrated areas of pigment along the midline and the bases of the dorsals are spread laterally. The trunk, posterior opercle, and the midline back to the posterior end of the anal are silver. The larger fish, as shown in figure 3, have the snout well-pigmented. The entire dorsal area above the level of the eye is uniformly dark brown. The top of the head is unpigmented except between the orbits. The dark pigmentation extends around the base of the caudal rays. The operculum and the lateral and ventral surfaces are silver. The anterior portion of the first dorsal (third to fifth spines) is black to the base. Spots have increased along the length of the fin so that the distal part to the last five spines is nearly black, but not so dark as the anterior part. The pigmentation extends nearly to the base at the posterior end of the fin. The second dorsal is pigmented from the base to about one-third of its height. The remaining fins are colorless. Except for lateral spots and bars this condition is similar to that found in the adult fish.

The lateral line is first seen in fish of 47 mm. total length. It is clearly visible only from its origin above the pectoral insertion to the region of the seventh dorsal spine. There is a slight upward curve over the pectoral. In a specimen 55 mm. long the lateral line is visible over its entire length. It curves obliquely under the soft dorsal and undulates just below the midline to the caudal peduncle.

In all specimens the body is laterally compressed and the head is prominent. The maxillary extends just posterior to the vertical bisector of the eye. The snout is long and pointed. In smaller fish the upper jaw is hooked and there is a distinct groove at the articulation of the premaxillary. The lower jaw is slightly shorter than the upper in fish up to 47 mm. in total length. The jaws are equal in fish of 55 mm. total length.

The preopercle has six spines in all but the largest specimen. These spines are prominent in specimens of 39 mm. total length. By the time the fish is 55 mm. long the spines are beginning to be overgrown, and at 71 mm. only three blunt spines remain. Hildebrand and Cable (1938:516) reported eight preopercular spines on *S. maculatus* 14 mm. long. These had become overgrown at 22 to 25 mm., so that only two preopercular spines remained and all spines were nearly overgrown at 35 to 40 mm. Ehrenbaum (1924) figured and described an undetermined species of *Scomberomorus* 73 mm. long from the Togo Coast, West Africa. This specimen had five blunt spines remaining on the preopercular margin. Munro (1943) figured two *Scomberomorus* (*Indocybium*) *semifasciatus*, 45 and 58 mm. total length, from Townsville, North Queensland, Australia. Preopercular spines were not indicated on these specimens.

My smallest specimen (21 mm.) has a fin-ray count comparable to that found in the adult. The first dorsal has 19 spines, the second dorsal has 2 spines

plus 13 rays followed by 9 dorsal finlets. The counts for the second dorsal rays and dorsal finlets may be one in error due to difficulty in determining which is the last ray and which is the first finlet. The anal has 2 spines plus 15 rays followed by 9 finlets. These numbers may also be one in error as in the second dorsal and dorsal finlet counts. In this 21-mm. specimen the finlets are joined to one another and to the fin by a membrane which reaches nearly to their distal ends. With increase in size the distal extent of the membrane becomes relatively less, so that at 71 mm. the distal half of the finlets is free. In the 61-mm. stained specimen the fin rays number as follows: First dorsal, 18 spines; second dorsal, 2 spines plus 16 rays and 9 finlets; anal, 2 spines plus 18 rays and 8 finlets; pectoral, 19 rays; ventral, 1 spine plus 6 rays. There is no indication of a lateral keel on fish up to 71 mm. in total length.

Teeth are prominent in all specimens, but relatively more so in the smaller ones. These have about 16 triangular, laterally-compressed teeth on each side of the upper jaw and about 9 on each side of the lower jaw. The 61-mm. specimen which was cleared and stained has 12 prominent teeth on each side of the upper jaw and 10 prominent teeth on each side of the lower jaw. Rudimentary teeth are visible in the dentary and premaxillary. A total of 46 teeth are present in the upper jaw and 31 in the lower jaw. No teeth can be detected on the vomer or palatines, although adults are known to have viliform teeth on both the vomer and palatines. (Jordan and Evermann 1896: 873; Meek and Hildebrand 1923: 321.)

Gill rakers are small and are merely bumps along the arch. Their number is difficult to determine in the small fish. Gill raker counts in the larger specimens are as follows:

Total length in millimeters	*Lower limb*	*Upper limb*
71	7	4
55	8	4
47	8	3
39	8	3
35.5	5	2

The liver is divided into three lobes. The right lobe is the longest and reaches one-half the length of the abdominal cavity. It is slightly attenuated at its posterior end. The other two lobes are comparatively short and thick. The stomach is large and reaches nearly the full length of the abdominal cavity. It lies above the remaining viscera. The caecal mass extends about one-third the length of the stomach. The right side is slightly extended. The intestine is straight except for one loop just posterior to its origin on the ventral surface of the stomach. Melanophores are present in the peritoneum.

In the 43-mm. fish which was cleared and stained, there are 20+28=48 vertebrae including the urostyle. In the 61-mm. specimen there are 19+28=47 vertebrae including the urostyle. This agrees rather closely with Starks (1910), who reported the vertebral count of a 24-in. *S. sierra* from Mazatlan, Mexico, as 19+29=48, excluding the hypural. Hildebrand and Cable (1938) reported vertebral counts for one specimen of *S. maculatus*, between 60 and 70 mm. long, as 23+30=53, and for another, 35 to 40 mm. as 22+31=53. A *Scomberomorus maculatus*, 167 mm. long, from Santos, Brazil, was X-rayed for a vertebral count [8] which was found to be 19+28=47. The structure of the vertebral column agrees generally with the description given by Starks for *S. sierra*. The first closed haemal arch is on the eleventh abdominal vertebra. Parapophyses

[8] This specimen was examined through the courtesy of Margaret H. Storey Natural History Museum, Stanford University.

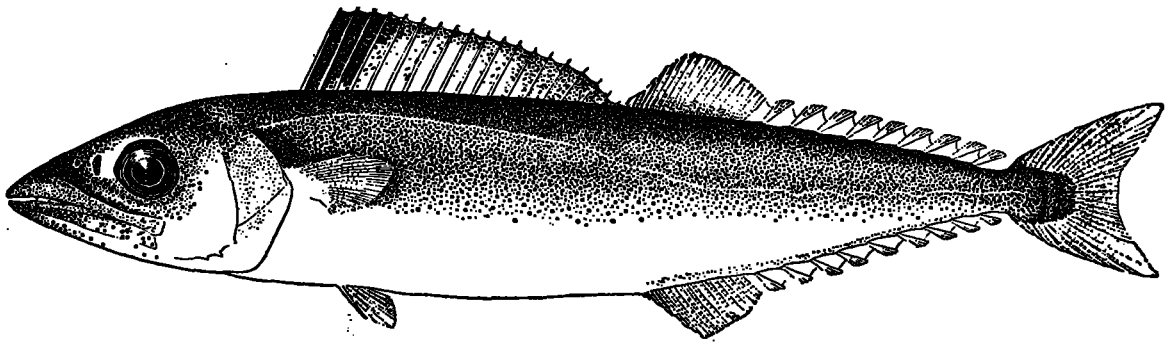

FIGURE 3.—*Scomberomorus sierra*, 71 mm. long.

are first developed on abdominal vertebrae 9 and 10. The haemal arches increase in length from the eleventh to the nineteenth vertebrae, where the first haemal spine appears. The first interhaemal is enlarged at the base and lengthened so that it extends to the base of the first haemal spine. Inferior foramina are developed on the bases of caudal vertebrae 12 to 26. These are small and are barely distinguishable on the more posterior vertebrae.

The specimens described herein may not all be *S. sierra*, as the various species of *Scomberomorus* are closely related and the young may not be separable at early stages. However, due to the rare occurrence of *S. concolor*, the only other species of *Scomberomorus* reported from the Pacific coast of North America, and the number of gill rakers in my larger specimens, it is probable that these specimens are *S. sierra*. A rather complete series of *S. maculatus* from the Atlantic coast of North America was described by Hildebrand and Cable (1938). The above specimens agree rather closely with the descriptions of Hildebrand and Cable for comparable sizes, except in the numbers of vertebrae and preopercular spines.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, Secretary
FISH AND WILDLIFE SERVICE, Albert M. Day, Director

BIOLOGY OF THE ATLANTIC MACKEREL (*SCOMBER SCOMBRUS*) OF NORTH AMERICA

PART II—MIGRATIONS AND HABITS

By Oscar Elton Sette

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BIOLOGY OF THE ATLANTIC MACKEREL (*SCOMBER SCOMBRUS*) OF NORTH AMERICA

PART II: MIGRATIONS AND HABITS

By OSCAR ELTON SETTE, *Aquatic Biologist*

The commercial catch of mackerel, *Scomber scombrus* Linnaeus 1758, along the Atlantic coast of North America has fluctuated widely (Sette and Needler 1934) owing to similarly wide changes either in abundance or in availability of the fish to fishermen. Since such fluctuations vitally affect both the fishery and the trade in its products, and also because they confuse the conservation problem, the United States Bureau of Fisheries (now a part of the Fish and Wildlife Service) in 1925 undertook an investigation of the causes of these fluctuations. The work involved not only studies of the fluctuations, but also of the many phases of life history and habits which had to be understood to interpret the observations of the changes in catch.

This report is one of several resulting from the mackerel investigations. In it there have been collected the facts that pertain to habits and migrations, particularly those that are pertinent to the understanding of changes in abundance or availability. The first number of this series of reports (Sette 1939) was on the early life history with special reference to mortality; others will be on age and rate of growth and on fluctuations in abundance.

In considering the subjects included in this paper it is necessary to draw on results which are to be reported later. This is particularly true with respect to the ages of certain size categories of mackerel. To a limited extent the data have appeared in preliminary reports (Sette 1931, 1932, 1933, and 1934) but for the most part the technical details are to be included in reports now in preparation and as yet unpublished.

ACCOUNT OF INVESTIGATIONS

The major conclusions of this report rest on the size composition of the mackerel population as determined from measurements of individual fish in thousands of samples drawn from the commercial catch at the principal ports of landing. The collection of data began in 1925 after part of that fishing season had elapsed. Much of the work in that year was preliminary in nature and not strictly comparable with subsequent observations. During the ensuing 10 years, 1926 to 1935, the program was carried out consistently so that data are comparable and the present report is confined to this period, except for the inclusion of certain data from tagging initiated in 1925.

The interviewing of fishermen for catch-date and locality and the sampling was done by Magnus I. Gregorsen in 1925, R. A. Nesbit in 1926, E. W. Bailey in 1927 and 1928, and by F. E. Firth in subsequent years. In many of the seasons R. A. Goffin contributed many samples from minor ports, principally Woods Hole, Mass., and also assisted in tagging experiments at that place.

Tagging of mackerel was recommended by the North American Council on Fishery Investigations and initiated under the supervision of Wm. C. Schroeder early in the 1925 mackerel fishing season, and after I undertook an investigation of the mackerel in all its phases during midseason of that year the tagging program was transferred to me. After completing the 1925 tagging season and upon comparing the size composition of the tagged fish with that of the samples taken from catches landed by mackerel vessels at Boston, it was obvious that the population from which the fish were drawn for tagging differed strikingly from the population upon which the vessel fishery was based.

This was not particularly surprising inasmuch as the tagging utilized fish from alongshore traps and pound nets whereas the vessel catch came mostly

from offshore schools. Since the vessel catch was by far the major element in the mackerel fishery as a whole (Sette and Needler 1934: 14) and presumably consisted of fish that were representative of the main population whereas the trap and pound-net catch presumably represented an inshore fringe of the main population, it was considered unlikely that tagging returns would be representative of the migrations of the population as a whole, or even of a very important segment of the whole population.

It also became apparent by the end of the first season's tagging that the tags were injuring the fish, with unknown effects on their survival and their migratory pattern.

For these reasons the emphasis on tagging was shifted from large-scale releases to small-scale experimental work directed toward improvement of tags and exploring the possibilities of tagging fish from the offshore population. The details of these experiments, in which I was ably assisted by R. A. Goffin in getting and caring for the fish in captivity and by R. A. Nesbit in developing ideas for devising and testing various tags, are given in appendix B.

The Biological Board of Canada kindly furnished records of mackerel tagged in Canadian waters and recaptured off the United States coast.

In the meantime the major activity of the investigation, aimed at discovering the causes for fluctuations in the mackerel catch, including the interviewing of fishermen, the measuring of samples of their catch and the collecting of catch records suitable for abundance indices proceeded regularly. By 1935, partial analysis of these data appeared to afford insight into many phases of mackerel biology and it was decided to report upon the material accumulated up to the end of the 1935 season.

In studying this wealth of material I have had the able assistance of Mildred S. Moses in preparing tabulations and performing computations, the helpful counsel of Henry B. Bigelow, and the use of facilities at the Harvard Biological Laboratories.

In 1937 the study of this subject was interrupted by other duties and could not be resumed until 1947, with facilities at the Stanford University's School of Biology and with the counsel of Willis H. Rich, at whose suggestion and encouragement the investigation was originally started in 1925.

SYNOPSIS OF RESULTS

The mackerel is found in the western Atlantic from North Carolina to the Straits of Belle Isle and is sufficiently abundant for commercial fishing from the Chesapeake Capes on the south to the Magdalen Islands and the Gaspé Peninsula on the north. During the season of fishing it is most abundant in the open waters of the inner third or half of the continental shelf.

The mackerel appears in April near the southerly end of its range and by July is found from southern New England to the Gaspé coast. In September it begins to disappear from the most northerly regions and in December it vanishes from all places. During the summer season the smaller and younger sizes are usually found closer to the shore line than the adults.

When mackerel disappear in the fall they go southward and offshore to the zone of warm water which flanks the outer edge of the continental shelf and during wintertime occupy this relatively narrow strip of water running more or less parallel to shore, but some 20 to 100 miles distant from it, from Cape Hatteras northward surely to the southern edge of Georges Bank and possibly as far as Sable Island. While there they probably occupy middepths and so are seldom seen or caught. In this location their food supply probably is uncertain and may depend on local swarms of plankton whose occurrence is irregular.

The pronounced schooling habit of the mackerel is dependent on a special tropism involving vision, and hence schools may disband and reform according to diurnal variations in light. Luminescence probably is important in keeping schools together at night in the spring and fall. Schooling tends to be according to sizes, perhaps owing to a connection between size and swimming ability. This in turn is probably dependent on the ratio of volume to surface which of course increases with size of body.

During spring, summer, and fall, the mackerel stay in the warm surface layer of the ocean because they are prevented from descending below the thermocline by the comparatively low temperature of the underlying waters. Variation in availability to fishermen, depending as it does on sighting schools at the surface, is therefore probably dependent on the varying depth of the thermocline. Fishing is best moderately close to shore where in summer the thermocline lies only 15 to 20 meters (8 to 11 fathoms) deep, and, as a rule, poorer farther offshore where the thermocline may be as deep as 40 to 50 meters (22 to 27 fathoms).

Mackerel feed principally on plankton but the

possibility that the larger individuals may in late summer subsist mainly on young fishes should be examined. Feeding is so much better in the summertime than in winter that the fat content of mackerel increases from a minimum in April to a maximum in August.

Two subdivisions are detectable in the western Atlantic mackerel population: A southern and a northern contingent which perform different spring migrations, occupy different areas in the summertime, and withdraw in the fall by different routes. The southern contingent comes from its offshore winter habitat toward the Virginia, Maryland, and New Jersey coasts in April, thence migrates northeastward to occupy the western part of the Gulf of Maine in summer. The northern contingent migrates toward the southern New England coast in May and thence goes northeastward to occupy the Gulf of St. Lawrence in summer. During the spring migration both contingents are joined by additional members of their kind which move from offshore directly toward the coast joining the main bodies as they pass along on their northeastward journey. For a short while in May both contingents are together in the area off southern New England, otherwise their courses are fairly independent. In the fall migration, both contingents approximately retrace their spring courses in returning to the winter habitat; but the northern contingent travels through more westerly waters in fall than in the spring, passing through the western part of the Gulf of Maine, and then disappearing off Cape Cod. The southern contingent, on the other hand, disappears, sometimes north of and sometimes west of Nantucket Shoals. The disappearance of both contingents north of the areas of their spring appearance may be due to their descent to deeper levels as the thermocline is lowered or obliterated by autumnal chilling.

DISTRIBUTION

RANGE

The mackerel is found on both sides of the Atlantic in the Northern Hemisphere, extending from the Mediterranean Sea to Norway in the eastern Atlantic and from North Carolina to Newfoundland in the western Atlantic. Since those of the eastern Atlantic are racially distinct from those on the western side (Garstang 1898), we need not consider them here.

The southernmost record on this side of the Atlantic is of two individuals taken in a pound net near Beaufort, N. C. The northern limit is the Strait of Belle Isle.[1] Reports of mackerel along the south and west coasts of Newfoundland are not uncommon, but occurrence seems not to be consistent enough to support a regular fishery for mackerel in Newfoundland. The region habitually occupied (in the fishing season) is from the Chesapeake Capes on the south to the Magdalen Islands and the Gaspé Peninsula in the Gulf of St. Lawrence on the north; in other words, between the thirty-seventh and forty-ninth parallels of north latitude.

Although the mackerel is distinctly an open-sea species, it is rarely found beyond the waters overlying the continental shelf; and while mackerel have been found at one time or another in the waters overlying the entire shelf, the greatest concentrations during the fishing season appear to be within its inner third or half. Often mackerel are found very close to the shore line, occasionally even inside of harbors and inner estuaries. Usually it is only the small sizes that are found in the semi-enclosed waters, the adults generally keeping to the open water, though they too enter some of the more or less open bays in the spring.

It is difficult, if not impossible, to determine whether the species is more abundant in the southern half of its range (that is, off the coast of the United States) than it is in the northern half of its range (that is, off the coast of Canada). Of the total annual catch along the North American coast in recent years, more than two-thirds have been taken off the coast of the United States and less than one-third off the coast of Canada; but this does not necessarily reflect the relative abundance, because the principal methods of fishing and also the intensity of fishing differ widely in the two countries. In the United States there is a fishery by pound nets and traps along shore, a minor offshore fishery using drift gill nets, and also a much more important offshore fishery using purse seines. In Canada fishing is confined almost entirely to pound nets, traps, and gill nets operated almost exclusively in inshore waters. It is likely that the international boundary, extended seaward, would divide the mackerel population into parts that are more nearly equal than total catch statistics indicate.

[1] Hearsay evidence cited by Goode, Collins, Earle, and Clark (1884: 3–4) of occurrence farther north along Labrador has yet to be confirmed by authentic records of capture.

SEASONAL CHANGES IN DISTRIBUTION

Along the Atlantic seaboard of North America the mackerel is a seasonal visitor, appearing in the spring, remaining during summer and autumn and then disappearing. Judging from the location of catches, mackerel appear first early in April about 30 to 40 miles offshore abreast of the coast line between Chesapeake and Delaware Capes. Soon they approach closer to the coast and during April and May they are found successively farther up coast until they reach southern New England. At this time or shortly afterward they also appear along the Nova Scotian coast. During the ensuing 2 to 4 weeks they disappear from the waters south of Cape Cod and spread throughout the western portions of the Gulf of Maine and the Maritime Provinces of Canada up to the Gaspé Peninsula, where they remain until sometime in September. During that month they begin to disappear from the most northerly region and withdrawal proceeds from north to south during October and November until finally in December they disappear from all coastal waters. These changes in distribution are charted, by months, in figure 2.

While the above description holds true for mackerel generally, there are differences that should be

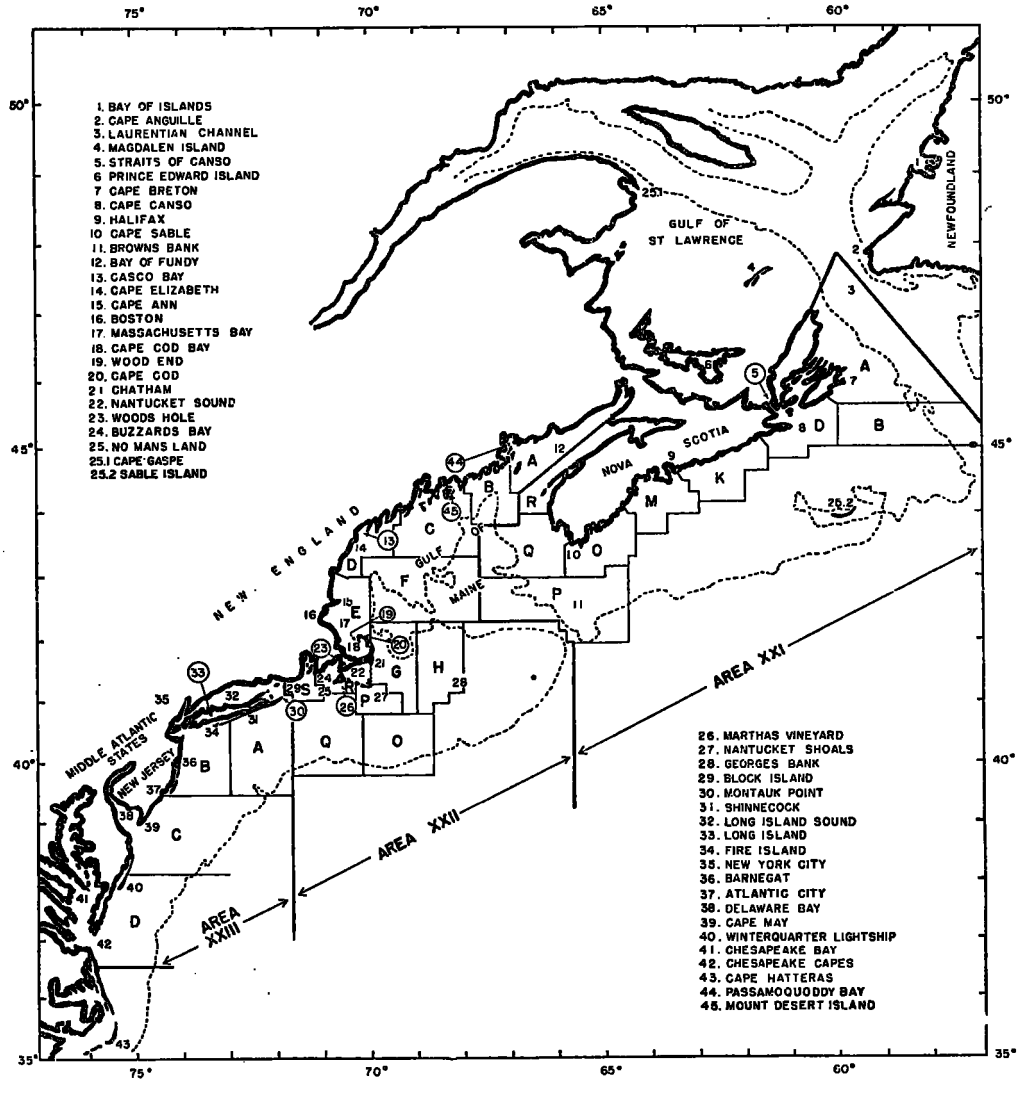


FIGURE 1.—Geographic features, landmarks, and delineation of statistical areas mentioned in this report. The statistical areas are those adopted by the North American Council on Fishery Investigations except for the lettered subareas of area XXVIII which were adopted for the purpose of this report, only, and have no official status. The broken line marks the 100-fathom contour.

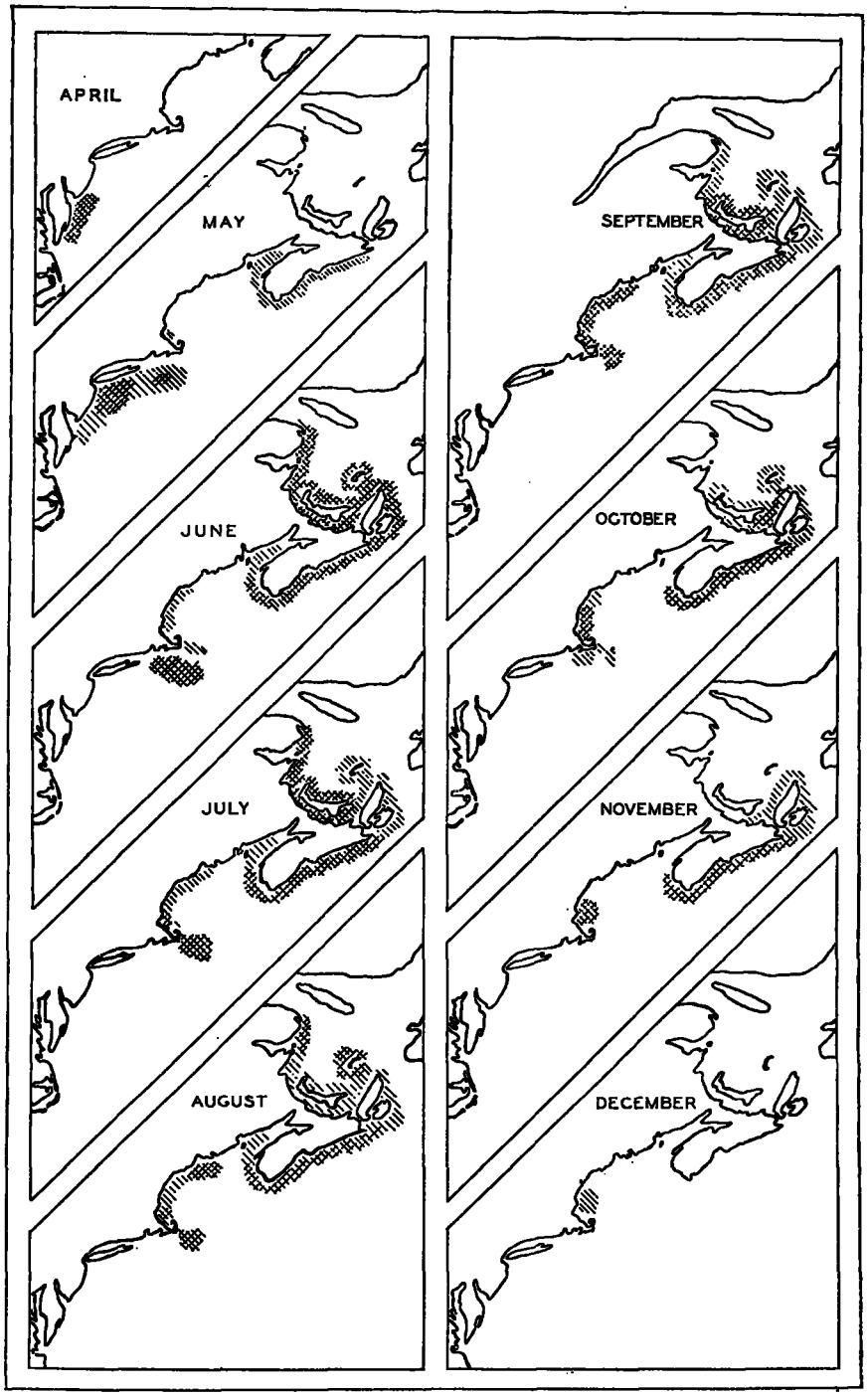


FIGURE 2.—Approximate seasonal distribution of the mackerel as indicated by location of the commercial fishery in the various months of the fishing season.

noted in the distribution of various size categories: (1) Juveniles, (2) yearlings, and (3) adults.

The juvenile sizes are fish from the current spawning season, hence less than a year old, and range from 2 inches up to about 8½ inches in length. Early in summer they are too small to be retained by the meshes of commercial nets, but toward late summer and fall, though not sought after, they are

caught incidentally. To fishermen they are known as "tacks" and "spikes." Drift-gill-netters never take them in quantities, though we have an occasional sample of fish whose teeth caught in the twine of gill nets. Purse seiners usually avoid them because they plug the meshes of the seine, sometimes causing loss of gear. Some of the largest sizes of juveniles are, however, caught by purse seiners late in fall. Pound nets, traps, and weirs are the form of gear taking them most consistently. The schools of juveniles are deflected by the coarse-meshed leader of these forms of gear and turn offshore into the fine-meshed pound, where the smaller ones may be taken by dip net before they slip out through the meshes while the pound is hauled; the larger ones, of course, are retained through the hauling process and regularly form a part of the commercial catch. It is the catch by this form of gear that provides most of the information on distribution of juveniles. Due to the selective nature of fishermen's catches of those small sizes, the conclusions must be inferential.

Their distribution early in summer is probably determined largely by the location of the grounds on which they were spawned and on their subsequent drift from these grounds (Sette 1939: 83–191). In United States waters, they are found most consistently along the shore from Long Island to Cape Ann. The maximum concentrations appear along the southern shore of Massachusetts, though some have been occasionally taken along the coast of New Jersey and the coast of Maine. Doubtless, such as survive on the spawning grounds of the Gulf of St. Lawrence would be found along the shores of that Gulf, presumably mostly along its easterly portions, but published records of this are lacking.

Although the available records of occurrence are almost entirely from along the very shore line, this may be because there is no form of gear employed offshore which will catch the juveniles. Late fall catches of these sizes by purse seiners sometimes have been at a moderate distance from shore (up to 20 miles) and it is probable that large bodies of these small mackerel exist offshore as well as inshore.

In the inshore locations, the juvenile mackerel seem to stay all summer, into late fall and even early winter, catches of them having been made as late as December. From their distribution, there is little indication of any extensive migrations before their disappearance.

Yearling mackerel range from about 20 centimeters (8 inches) in the spring to about 35 centimeters (14 inches) in late fall. They are called "blinks" and "tinkers" by fishermen and in the trade. The term "blinks" is usually applied to the smaller ones, "tinkers" to the larger ones of this category.

During summer and fall, their distribution parallels that of the adults (p. 254) but their appearance in the spring is usually later than that of the adults. Occasionally schools are taken during the spring run of adults in both pound nets and purse seines (drift gill nets almost never take them at any season); but it is not until July and August that they are taken regularly in large numbers. From that time onward they are taken all along the coast from southern Massachusetts to Maine. Although samples of yearlings have been secured from Passamoquoddy Bay and from the vicinity of Halifax (Pennant, Nova Scotia), Dr. Cox found no "small" mackerel at the Magdalen Islands in 1925 (North American Council on Fishery Investigations, 1932, p. 27) and samples taken during this investigation from the catches of United States mackerel purse seiners fishing off the Nova Scotian coast have never contained yearling mackerel. It is likely that yearlings are much less abundant, as a rule, off Canada than off the United States. Like the juveniles and the adults, the yearlings disappear from coastal waters in late autumn and early winter.

The adult mackerel are known simply as mackerel by the fishermen, sometimes with the qualifying adjectives "medium" or "large." They are fish of 35 centimeters (14 inches) and upward and include all aged 2 years and older. They are the most desirable sizes and usually form the bulk of the catch. Their distribution corresponds with the general description at the beginning of this section.

WINTER HABITAT

LOCATION

Whence the mackerel come in the spring and whither they go in the autumn have been subjects of conjecture for many years. Bigelow and Welsh (1925: 197) surmised that they winter "on the upper part of the continental slope at a depth rather greater than the otter trawlers reach—say at 100 to 200 fathoms—but so close at hand that odd fish stray or remain on the banks." The present available data support this view as to the general winter location. It suggests, however, somewhat different conclu-

sions as to the depths inhabited in the wintertime.

That the late autumn chilling of the water drives the mackerel from their customary summer haunts appears so obvious that most investigators have accepted this assumption as fact. It is true that the months during which the mackerel are absent are the coldest months of the year but there is no experimental evidence as to the minimum temperature that can be withstood by the species. As far as observational evidence is concerned, mackerel have been found in abundance in temperatures as low as 8° C. (fig. 14). They are often present in water of 7° C. in sufficient numbers to make commercial fishing profitable. Below this temperature they have been taken only as stragglers in American waters where there is record of one occurrence in water as cold as 4.5° C.[2] Thus it appears that the American mackerel prefers temperatures above 8° C., that it frequently tolerates temperatures down to 7° C., and that its toleration may extend to temperatures as low as 4.5° C.

This being true, the winter temperature in the northern portion of its range, that is in the Gulf of St. Lawrence and along the inner portions of the continental shelf of Nova Scotia where ice often forms in the wintertime, is certainly too low for this species. The inner parts of the Gulf of Maine with winter temperatures from 2° to 3° C. must also be too cold for mackerel. South of Cape Cod in cool winters when temperatures of 2° to 4° C. usually prevail over the inner half of the continental shelf, the mackerel should be normally absent; but there are instances such as the winter of 1932 (Bigelow 1933: 8–27) when water as warm as 7° C. persisted throughout the winter almost to the shore line and north nearly to New York. Obviously, temperature alone cannot explain the absence of mackerel from these waters during such exceptionally warm winters, and thus we may not assume their disappearance in the fall to be a simple direct response to temperature.

Yet it is reasonable to look for their winter habitat where temperatures approach those prevailing in their summer habitat. Waters with such temperatures flank the North American coast from 30 to 100 miles offshore, their inner border lying near the edge of the continental shelf where depths increase rapidly beyond the 100-fathom contour (fig. 3). It is not necessary to look farther than this, for mackerel have never been found south of Beaufort, N. C., or far enough beyond the continental shelf to indicate that they wander far out into truly oceanic waters.

The constancy in location and warmness of this flanking zone of water as a regular winter home for the mackerel is of particular significance. Although the temperatures of each profile in figure 3 pertain to only 1 year, it is highly probable that the warm zone has the same position year after year. This is certainly true along the continental edge between Cape Cod and Cape Hatteras. This region has been examined hydrographically in five different winters with very little variation except in the unusually warm winter of 1932. In that year nearly the entire continental shelf south of the middle of New Jersey was covered with water 7° C. or higher, but even then the temperatures at the edge of the shelf were very little different than in cold winters. Hydrographical surveys of the southern edge of Georges Bank in the winter have been less frequent, but examination of early spring conditions in 1929, 1930, and 1931 reveal no striking variations.[3] It may be assumed, therefore, that the mackerel can always find temperatures surely suited to its existence at one depth or another by moving offshore to about the continental edge along the southern part of Georges Bank or to the outer third of the continental shelf between Cape Cod and Cape Hatteras, and possibly suited to its existence along the edge of the Nova Scotian Banks. It remains to be seen what direct evidence there may be of the actual presence of mackerel in this warmer zone.

The occasional capture of mackerel incidental to the fishery for other species in the winter has been reported often in the literature. Goode, Collins,

[2] In European waters, large quantities have been taken by trawlers in northern parts of the North Sea, notably Great Fisher Bank, in the wintertime when 6° and 7° C. water prevails on those grounds, and in the English Channel where they are also trawled in the wintertime, the temperatures according to Bullen (1908: 284–285) are between 8° and 9° C. However, the European mackerel differs structurally from the American mackerel, sufficiently to be regarded as racially distinct, so it may be physiologically different as well. Hence, it is wise not to lay much stress on the evidence provided by the European representatives of the species.

[3] Unfortunately, there are no data on an extremely cold winter when it is possible that the warm zone may shift to a more offshore position. The disappearance of the tilefish in 1881 (Bigelow and Welsh 1925: 354) has been thought to have been caused by such a shift and if this supposition is correct, it must mean that the warm zone shifts far enough offshore so that it does not come into contact with the sea bottom at the continental edge. However, just as the tilefish disappearance may be taken as evidence of possible offshore shifting of the warm zone in severe winters, it also constitutes evidence that such shifts are extremely rare, for as far as is known this has happened only once during the past century. Even then it apparently had no effect upon the mackerel which may have been wintering on or near the tilefish grounds, for mackerel reappeared in normal numbers during the summer following the tilefish disappearance.

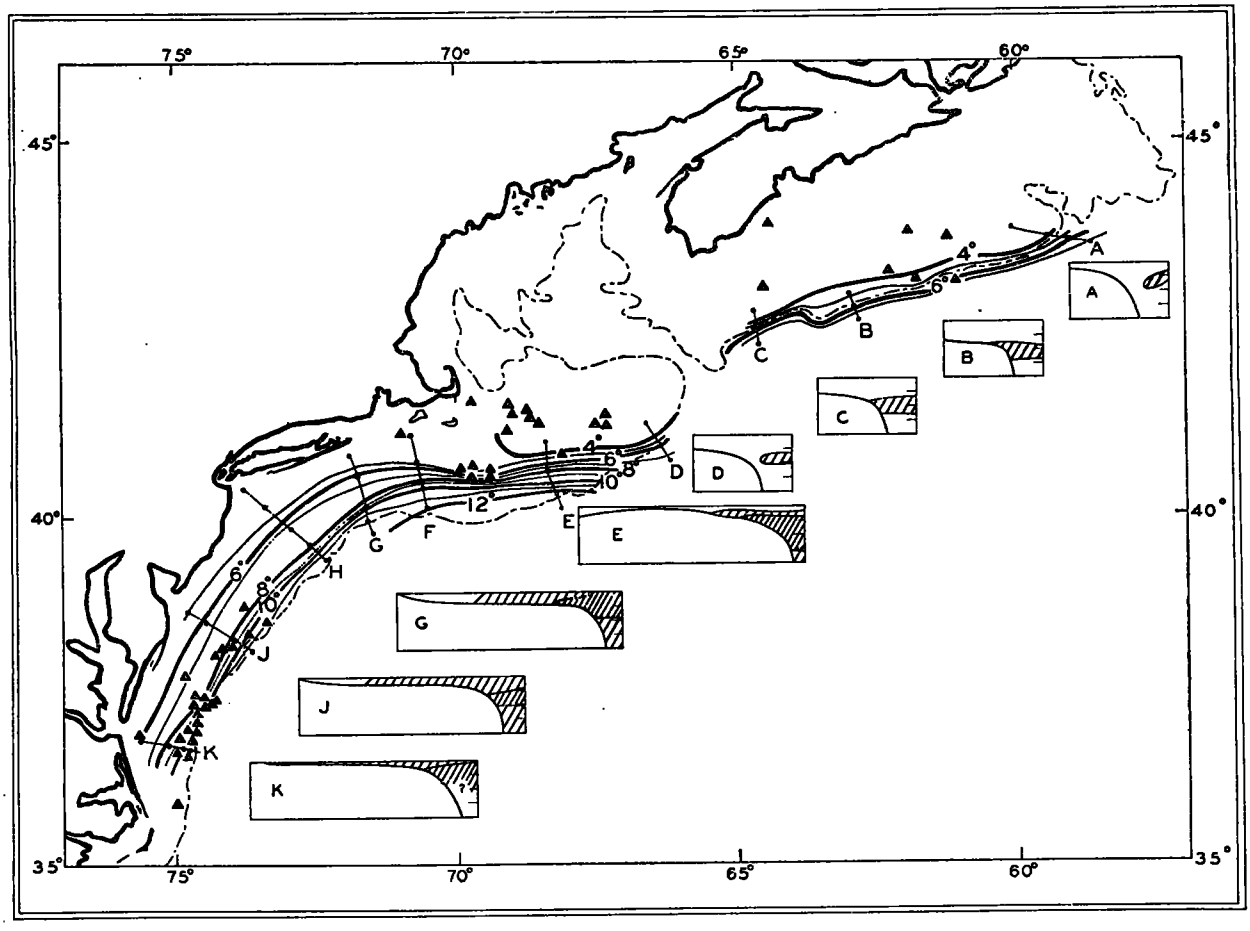


FIGURE 3.—Winter captures of mackerel (triangles) and winter temperatures. The isotherms mark the greatest inshore extension of water of designated temperature; insets A to D represent a width of 80 miles, E to K a width of 35 miles, and all represent depths of 400 meters (218 fathoms). Light shading designates temperature above 6° C. and heavy shading temperatures above 10° C. Sources of temperature data are: Section A, C. G. S. *Acadia* Stations V, 6–8–9–10, May 30, 1915 (Bjerkan 1919: 384). Sections B and C, *Atlantis* Stations 2510–11–12–15–16–17, March 6 and 15, 1936 (Bull. Hydrographique Cons. Perm. Internat. pour de l'Explor. de la Mer). Sections D and E, *Albatross II* Stations C20044–45–46–47–66–67–68–69, March 11–12 and 22–23, 1920 (U. S. Bureau of Fisheries Rept. 1921: 154, 160). Section F to K, *Albatross II* Stations 20618–19–20–21–22–23–24–25–26–28–29–30–31–32–34–35–36–37–40–41–42–43, Feb. 5–10, 1930 (Bigelow 1933: 113).

Earle, and Clark (1884: 98) list 7 or 8 taken in a gill net on Georges Bank on a January 3 or 4, a number taken by a schooner on Georges Bank, in March 1856, tinkers taken from the stomachs of cod, sometimes 5 or 6 from one fish, and used for bait on Georges Bank in February 1878; 30 caught on a trawl line set on Middle Bank in January 1868 or 1869, and "two fine fat fresh mackerel were found among the kelp at Green Cove on Friday, December 28, 1878," reported by the Yarmouth (Nova Scotia) Herald. Bigelow and Welsh (1925: 196) give additional instances of mackerel taken from cod stomachs on Georges and La Have Banks and off the coast of New Jersey in winter, also occasional catches by otter trawlers in the South Channel and on Georges Bank in February and March. Such records can now be augmented materially by instances that have accumulated during the course of the present investigations. These are listed in table 1, and their positions appear in figure 3.

TABLE 1.—*Winter records of mackerel*

Locality	Date	Depth (fathoms)	Quantity	Size	Remarks
In the offing of Nova Scotia:					
Western Bank, 50 to 100 miles west of Sable Island.	Jan. 9–16, 1931			12–15 centimeters	Lot of pollock containing a number of small mackerel.
Do	do		2	Large	
Do	do		Few	Small	
La Have Bank	Dec. 12, 1931		100 pounds		
Lat. 43°10′ N., long. 61°40′ W	Feb. 3, 1932	4–5	95 pounds	26.8–28.7 centimeters	
Lat. 43°50′ N., long. 61°50′ W	Feb. 15, 1932	32–60	100 pounds	Tinker	
Lat. 43° 45′ N., long. 61°10′ W					
Lat. 43°05′ N., long. 64°25′ W	do	50–60	75–100 pounds	Small	
Lat. 43°20′–30′ N., long. 62°5′–15′ W	do	50–70	60 pounds		
Lat. 43°55′ N., long. 64°25′ W	Feb. 1, 1934	70	5	15–20 centimeters	Found alive in stomachs of hake and pollock.
Emerald Bank	Jan. 8, 1935	30–42	1	1½ pounds	
North of Emerald Bank	Feb. 14, 1935	53–55	Many	13–15 centimeters	
Lat. 43°15′ N., long. 61°00′ W	Mar. 13, 1935	50–60	35	About 2½ pounds	
Browns Bank	Mar. 28, 1935	60	1	41 centimeters	
In the offing of New England:					
Georges Bank	Jan. 18, 1929		36	Small	
Lat. 41°11′ N., long. 69°00′ W	Feb. 9, 1929	50	1	48.5 centimeters	Debris and mucus in stomach.
Do	do	50	3	Tinker	In stomach of a pollock.
60 miles southeast Highland Light	Mar. 12, 1929	70	1	44 centimeters	Stomach empty.
Do	do	70	6	Tinker	
7 miles south of South Shoal Lightship	Dec. 23, 1929		100 pounds	1½ pounds	
Southeast part of Georges Bank	Jan. 21, 1930	42	1	32.5 centimeters	Very thin.
90 miles southeast Highland Light	do	38	1	31 centimeters	Very thin; stomach empty.
80 miles southeast Highland Light	Mar. 31, 1930	36	1	30 centimeters	Very slender; much sand on lls, gill rakers, and mouth.
Southeast part of Georges	Jan. 10, 1931	27	1	21 centimeters	
Southeast ½ east Highland Light	Jan. 16, 1931	28–30	12	17.5–21 centimeters	
78 miles southeast ½ south Highland Light	Jan. 21, 1931	60	1	44.2 centimeters	Weighed 2 pounds in round condition.
Lat. 40°50′ N., long. 68°00′ W	Jan. 22, 1931		19	12–20 centimeters	In pollock; cod and haddock also eating them.
Southwest Georges	Mar. 25, 1931		40	Tinker	
Do	do		1	19 centimeters	In stomach of a haddock.
Georges Bank	Dec. 21, 1931		65 pounds		
Do	Jan. 1, 1932		1	Large	
Off South Shoal Lightship	Jan. 7–14, 1932		200 or 300	Mixed	Fishing boats report catching a number of mackerel of mixed sizes. 1 steamer got as many as 200 or 300.
Lat. 40°40′ N., long. 69°50′ W	Jan. 5–13, 1932		1		
Lat. 40°40′ N., long. 69°20′ W	do		174	17–40 centimeters	Temperature 4.5° C.
Lat. 40°30′–40′ N., long. 69°20′ W	do		66		
Lat. 40°40′ N., long. 69°20′ W	do		12		11 were in stomach of 1 pollock; 1 in stomach of another.
Lat. 41°35′ N., long. 69°40′ W	Feb. 15, 1932	60–75	35 pounds	Small	
Lat. 41°20′–30′ N., long. 68°30′–50′ W	do	70	12	Large	
Lat. 41°10′–30′ N., long. 69°00′–10′ W	do	45–60	About 6	Tinker	
		90	do	Large	
Georges Bank	do		About 50		
Do	Feb. 19, 1932			Large and tinker	A number of vessels caught mackerel both large and tinkers. A large school of large mackerel was sighted.
South Channel	Mar. 23, 1932		120 pounds		
Lat. 41°10′–20′ N., long. 67°10′–20° W	Dec. 3, 1932	26	1	31.6 centimeters	Temperature 10.5° C.
Lat. 41°10′–20′ N., long. 67°20′–30° W	do	27–31	18	17.1–20.3 centimeters	
Lat. 41°20′–30′ N., long. 67°10′–20′ W	Dec. 6, 1932	27	2	30.7 and 34.4 centimeters.	
Lat. 41°10′–20′ N., long. 67°10′–20′ W	Dec. 7, 1932	27	1	19.2 centimeters	
Nantucket Shoals	Dec. 12, 1932		290 pounds		
Do	Dec. 23, 1932		300 pounds		
20 miles southwest of No Man's Land	Dec. 5, 1934	29	50 pounds	All sizes	
Southeast part of Georges Bank	Jan. 9, 1935	35–45	4	Medium	
Lat. 40°41′ N., long. 69°40′ W	Dec. 3, 1935	27	51	14–24 centimeters	Temperature 7.3° C.
In the offing of the Middle Atlantic States:					
Lat. 38°13′ N., long. 73°49′ W	Mar. 2, 1931	52	9		In hake stomachs; 4 in 1, 3 in 1, and 2 in 1.
Do	do	52	1	Small	In hake stomach.
180 miles south of Cape May, 30 miles east of Bodie Island.	Mar. 10, 1931	30	1	25	
70 miles south ¼ west Winterquarter Lightship.	Mar. 17, 1931	57	1	10 centimeters	"Spike."
52 miles east by south Cape Charles	Feb. 2–3, 1932	43–59	6	Small	3 to pound.
45–50 miles east by south Chesapeake Lightship.	Feb. 13, 1932	42–46	3	Small	2 in hake stomachs.
65 miles east-northeast Chesapeake Lightship	Feb. 17, 1932	38–60	Several	Small	
45 miles east by south Chesapeake Lightship	Feb. 25, 1932	38–40	1	Small	
20 miles southeast Winterquarter Lightship	Apr. 7, 1932	35–40	18	25.5–42.5 centimeters	Thin and in poor flesh.
Lat. 36°50′–60′ N., long. 74°30′–40′ W	Jan. 4, 1933		1	44.5 centimeters	Very large and fat.
60 miles east by north ½ north, Chesapeake Lightship.	Jan. 12, 1933	45	1	30–35 centimeters	Large, in good condition, showed fatness.
40 miles east ½ south Chesapeake Lightship	Feb. 3, 1933	45	1	31.5 centimeters	Very thin. Crustacea and worms in stomach.
62 miles east-southeast Cape May	——, 1933	40	About 50	50 centimeters	Very large and fat. Stomachs crammed full of shrimplike crustacea 1 inch long.
50 miles east by south Chesapeake Lightship	Feb. 19, 1933	32	1	33 centimeters	Stomach partially filled with fragments of copepods, Euthemisto, and unidentified fragments.

TABLE 1.—*Winter records of mackerel*—Continued

Locality	Date	Depth (fathoms)	Quantity	Size	Remarks
In the offing of the Middle Atlantic States—Con.					
100 miles northeast by east Chesapeake Lightship.	Feb. 18, 1934	60	1	2 pounds	Thin.
58 miles east by north—east by north ½ north Chesapeake Lightship.	Mar. 3, 1934	51–60	3	37–45 centimeters	
45 miles east ½ north Chesapeake Lightship	Mar. 4, 1934	58	1	46 centimeters	
106 miles northeast by east Chesapeake Lightship.	Mar. 12, 1934	43–50	10 pounds		
70 miles east by north ½ north Chesapeake Lightship.	Mar. 23, 1934	60–65			Very thin.
63 miles east by north ½ north Chesapeake Lightship.	Mar. 28, 1934	55–63	7	29–39 centimeters	
65 miles east-southeast Five Fathom Lightship.	Feb. 8, 1935	58	20 pounds		
East-southeast Cape Henry	Feb. 14, 1935	90	2 tinkers, 1 large		
55 miles east by north Chesapeake Lightship	Mar. 2, 1935	55	11 pounds	29–44 centimeters	
100 miles southeast Cape May	Mar. 28, 1935		35 pounds	1–2 pounds	

The significance of these records must be weighed in relation to the distribution of fishing in the wintertime, for the lack of records from any particular area would be meaningless unless fishing took place in that area. Thus, the lack of winter catches along the southern edge of Georges Bank is due to the failure of fishermen to trawl there.[4] Similarly, the dearth of any winter records between the western portion of Georges Bank and the offing of Delaware Bay has no significance because no fishing takes place near the edge of the shelf in this sector during the wintertime. From about the offing of Delaware Bay to Cape Hatteras, on the contrary, numerous otter trawlers fish intensively during the entire winter along the continental edge and accordingly there are a number of instances in which mackerel were caught on these grounds. Thus, where fishing takes place in the warm zone in the wintertime, mackerel appear in the catch, and only portions of the warm zone that are not fished in the wintertime fail to contribute winter mackerel records.

There are, however, two features of this series of winter records that are contrary to the theory that the warm zone constitutes the winter habitat of mackerel. These are, first, the numerous specimens of mackerel taken on Georges Bank and along the coast of Nova Scotia considerably inshore of the warm zone and in water that presumably was much colder than is considered suitable for mackerel, and secondly, that even in the sector between the offing of Delaware Bay and Cape Hatteras where mackerel have been taken by otter trawlers, the numbers encountered are so very few that they cannot be taken as representing the main body of the mackerel population.

Since it is hardly likely that there are warm pools or lateral extensions of warm water along the bottom on Georges Bank (hydrographers have never encountered them), the records of mackerel well up on the bank must be accepted as evidence of their presence in rather cold water; indeed one of the catches was made in water that tested 4.5° C. at the time. Either our notions of the temperatures tolerated by mackerel are erroneous, or for brief periods of time small groups may stray away from the main population. That these records of stray mackerel exist is more likely owing to the thoroughness with which the waters there are dredged by the trawlers rather than to the occurrence of quantities of mackerel.

Winter catches of mackerel in the sector in the offing of the Middle Atlantic coast between Delaware Bay and Cape Hatteras nearly all fall within the warm zone at the continental edge as might be expected. Although their location agrees well with the theory set forth above, the number of records and the quantities of fish taken are far too low for a region supposed to harbor the main bodies of mackerel in the wintertime and where winter trawling is intensively practiced. This can hardly be attributed to deficiencies of the otter trawl as a means of catching mackerel for mackerel are regularly taken by trawl in the wintertime along the slope of the North Sea plateau toward the Norwegian Channel and in the English Channel. Hence it must be concluded that the American mackerel are not concentrated near bottom in the wintertime.

It is also apparent that mackerel are not at the surface in the wintertime as has often been remarked upon in the literature. Exceptional reports of the

[4] During the period 1931–33 the location of fishing during each trawler trip was ascertained in connection with the Bureau of Fisheries investigation of the haddock fishery. Among the thousands of fishing locations which were recorded only one fell within the area bounded by the 6° C. isotherm and the edge of the bank.

sighting of such schools as have appeared in the literature may be discounted (Bigelow and Welsh 1925: 196) on the basis that the reports are not authenticated by specimens from such schools, the inference being that some other scombroid or even clupeoid species was concerned. Furthermore, mackerel fishermen often have striven to extend the fishing season by searching for fish earlier in the spring and later in the fall than the regular season. During the 10 years of this investigation when the activities of the mackerel fleet were under close observation, seiners have scouted in early spring farther to the south and farther offshore than the area in which the first catches are customarily made. In the fall also, they have often persisted in looking for mackerel some weeks after the final catches were made; and although such searches extended farther offshore and farther southward than the ordinary range of the fishery, they have been in vain.[5] Then too, the trawlers that frequent the warm zone in the offing of the Chesapeake Capes each winter would surely recognize mackerel schools if they saw any, for these same fishermen, as a rule, engage in mackerel fishing in the summertime and would not only be quick to report any schools sighted in the wintertime but also would very likely outfit for seining and try to catch them, for the winter prices would make the fishery quite lucrative if considerable quantities could be caught. Hence it must be concluded that mackerel in disappearing in the fall, sink below the surface [6] and if they reappear at the surface subsequently, it is only for short periods of time and at infrequent intervals.

In summary, it may be concluded that the winter home of the mackerel is in the warm zone along the continental edge from Cape Hatteras to the middle of the southern edge of Georges Bank, for here the water is surely warm enough and enough stragglers have been taken to indicate that the main population is nearby. It may possibly extend even as far to the northeast as the offing of Sable Island, for 6° C. water extends that far and stragglers have often been taken on the Nova Scotian banks in the wintertime. Although present in this zone of warm water, they do not regularly appear at the surface nor do they stay close to the bottom. In all probability they are in middepths, perhaps above rather than below about 100 fathoms. Whether their schooling habits are preserved in the wintertime or whether the individuals are widely scattered, must remain a mystery probably until means of fishing the middepths have been devised.

PROBABLE CONDITIONS OF EXISTENCE IN THE WINTERTIME

Whether or not food is of any consequence to the mackerel in wintertime is called into question by early theories of hibernation of the mackerel which include such fanciful suppositions as inspired the statement of a French Admiral whom Ehrenbaum (1914: 10) quotes as declaring that "his men had seen thousands of mackerel in the bays of the Greenland coast in the spring, the fish having buried their heads in the mud, and hibernating in that position, as a result of which they became blind, and were thus very easily caught." Needless to say, such evidence of the mackerel's food requirements in the wintertime need not be taken seriously, since mackerel are now known not to inhabit Greenland waters; but Ehrenbaum, whose extensive study of this species entitles his views to great respect was not convinced that the European mackerel may not be in at least semihibernation during the wintertime, for he stated (1914: 13):

> There is thus no longer any doubt that the mackerel at certain seasons of the year seek the bottom, and the lower water layers, and although they do not appear to spend the whole of this period in passive hibernation, but rather to be, at times, eager for food, it is nevertheless highly probable that they hibernate for a part of their stay at the bottom, viz, from November to January, when, according to the observations of Irish investigators, as also my own, the taking of food is as a rule suspended. During this time, the stomachs of mackerel taken with the trawl are found to be entirely empty, and not until February and March do we find a slowly increasing percentage of fish containing food.

Bigelow and Welsh (1925: 197), commenting on Ehrenbaum's view of mackerel hibernation, say:

> It is not likely, however, that the American mackerel do so, though they may be semitorpid or at least very sluggish during the cold season, the presence of mackerel in the stomachs of other fish as well as the fact that they sometimes have food in their own stomachs in midwinter, proving that they move about more or less even then, though they certainly feed very little, for not only

[5] In December of 1932, for instance, schools of mackerel were reported from the easterly portions of Georges Bank and at least one seiner cruised to these grounds but failed to find the mackerel. Again in December 1933, the schooner *Old Glory*, Capt. Frank Foote, sailed to the southerly offshore grounds for mackerel and although a school was sighted 25 miles southeast of Fire Island Lightship, deficiency of the gear prevented a catch, and when the vessel reoutfitted and returned some days later, no mackerel schools were to be found.

[6] A bit of experimental evidence on this point is afforded by the action of mackerel held in a large outdoor pool at Woods Hole in 1932. These frequently were schooling at the surface during summer months but toward the end of September when the water cooled they stayed well below the surface and even when food was thrown on the water, appeared reluctant to rise to the surface as formerly was their habit. Unfortunately, the occurrence of a heavy rain flooding the harbor and making the water markedly turbid at this time leads to uncertainty as to whether turbidity, decrease in salinity, or lower temperatures caused the change in habit.

are most of the European fish trawled at that season empty, but European and American mackerel alike are thin when they reappear in the spring.

I agree with Bigelow and Welsh that there must be some feeding activity in the wintertime. If, as is supposed, mackerel at this season are at mid-depths, some activity would be required and some energy consumed in maintaining this position. That some of the needed energy is acquired currently by feeding is indicated by the food in the stomachs reported by Bigelow and Welsh, and observed by F. E. Firth during the present investigations. That they fare less well in winter than in summer and are forced to draw on stored energy, is proved by the low average fat content in early spring (p. 268). It also appears that not all portions of the population are equally successful (or unsuccessful) in obtaining food in the wintertime, for of the winter-caught specimens that came to the hands of F. E. Firth during the course of the present investigation, some were fat and some were lean. This suggests that food is not distributed uniformly, or that the concentrations of mackerel and of mackerel food do not always coincide.

What little is known about plankton (the principal food of mackerel) is consistent with the view that food is generally scarce in this area in the winter and that it may be spotty. In the Gulf of Maine, Bigelow (1928: 190–191) found *Calanus finmarchicus* (the dominant plankton species of the region and the most important food organism for mackerel) so scarce in February and March (1920) as to yield hauls of only 3,900 per square meter on the average. Whereas in May and June (1915) the average for all stations was 86,000 per square meter. Thus, in the Gulf of Maine, the winter populations of *Calanus finmarchicus* appeared to be less than one-twentieth as large as the summer population. On the continental shelf between Cape Cod and Chesapeake Bay, this copepod is also very scarce in the wintertime. Bigelow and Sears (1939: 306) found tow-net catches to be only one-eighteenth as large in February as in April 1930, and only one-twentieth-ninth, one-ninth, and one-tenth as large in February as in May of 1930, 1931, and 1932, respectively.

Not only is there a general scarcity of plankton in the wintertime, but the waters at the outer edge of the continental shelf where the mackerel are supposed to winter, have as little plankton as the waters farther inshore, and south of Cape Cod, even less. However, among all the plankton tows taken along the edge, both by Bigelow and by ourselves, there was one at the southern edge of Georges Bank that yielded 103,000 *Calanus* per square meter (Bigelow 1926: 190–191) which is an abundance comparable to spring or early summer in the Gulf of Maine. Bigelow regarded this as a local swarm. Towings along the continental shelf in the wintertime have neither been closely enough spaced to indicate how many such swarms exist at a given time nor have they been made at enough different times during winter to prove or disprove their existence as a characteristic winter phenomenon. Their occasional occurrence, suggested by the catch at the southern edge of Georges Bank, would not only enhance the suitability to mackerel of continental edge waters in the wintertime but would also account for the fatness of some winter-caught mackerel despite the leanness of most.

SCHOOLING HABITS

MECHANISM OF SCHOOLING

One of the most characteristic habits of the mackerel is its tendency to associate in dense schools. On the basis of observations and experiments principally on *Pneumatophorus grex*, a related species of similar schooling habit, Parr (1927) evolved the theory that the school is maintained by simple reactions which "may be regarded as automatically controlled by a special kind of tropism giving responses of approach and adjustment of direction to the stimulus of a perceived prospective companion." That perception is by visual means appears adequately proved by Parr's observations and experiments and has particular significance in connection with the formation and stability of schools.

As Parr pointed out, if the aggregation into schools depends on vision, it should take place during the daytime and the schools should be broken down during every sufficiently dark night. If this is true, the nightly reshuffling of individuals should tend to keep the population homogeneously mixed. At certain seasons, however, the break-down of schools obviously does not take place at night, for purse seiners locate and catch schooled mackerel at night both in the springtime and in autumn. At these seasons the schools are located by the luminescence which is associated with them. This occurrence of schools at night need not be contrary to Parr's theory, for obviously the luminescence may be as effective as daylight in permitting the visual per-

ception necessary for schooling. However, there should be a tendency toward greater permanence of schools in spring and autumn, which might be reflected in greater divergence between schools in respect to certain characters such as size-composition. This has not been so obvious for me to have noted it, but admittedly the data have not been collected or analyzed in a way which would be adequate to demonstrate this point.[7]

ADVANTAGES OF THE SCHOOLING HABIT

In addition to his inquiry as to the method in which the schools are maintained, Parr (1927: 31) discussed the usefulness to the species of the schooling habit, pointing out that if individuals of a much preyed-upon species like sprat or herring traveled around separately, "scarcely a single one of them would escape the enemies sufficiently long to be able to propagate, while the occurrence of a great number of specimens united in schools among scattered enemies may give a certain percentage a chance to survive and continue the existence of the species." This, however, overlooks the fact that the enemies of schooling fish often are banded together and thus tend to overcome this advantage of their prey.

In view of this, it appears to me more reasonable to suppose that the advantage of schooling, if any, would lie in the increased ability to capture prey rather than to elude predators. This is suggested by observation on the feeding activity of mackerel held in confinement in an outdoor pool open to tidal circulation (p. 352). When food was offered to these mackerel in the form of ground squid or fish, i. e., in relatively large particles compared with plankton, the mackerel darted toward certain particles and secured them individually. When feeding thus the schooling habit was broken down and although the individuals congregated in the vicinity of food their actions were not coordinated. On the other hand, when not so—feeding, the mackerel collected in a definite school coursing around the pool in a fair degree of unison though even at such times their actions were less concerted than when feeding on plankton. Such feeding took place very close to the surface, usually in calm weather and often in the early morning or late evening. At least it was most easily observed at such times.

When feeding on plankton the mackerel assembled in a much more compact school than at other times. The school swam in a path describing a small circle or ellipse perhaps 8 or 10 feet in diameter and lying in an inclined plane, the upper limb of the ellipse touching the surface, the lower limb about 2 or 3 feet deep. On the descending segment the individuals swam vigorously, perhaps at twice the speed customary in coursing movements, obviously getting up speed. As they returned up the ascending segment of the ellipse, they opened their mouths to the fullest extent and extended their operculums widely, obviously to pass the maximum of water past the gill rakers. In this condition the school formed a group of miniature tow-nets spaced hardly more than their own diameter apart. If it be supposed that copepods (the principal element in their diet) are capable of darting 1 or several centimeters at a time through the water, as observation indicates they do, they might elude one such miniature tow-net; but with a group of miniature tow-nets as closely spaced as these, the success of a copepod in eluding one of them would frequently only put it in the path of another. Thus mackerel, acting in concert probably would average more copepods each than if they acted individually.

This theory supposes that the copepods and other planktonic food organisms are capable of detecting a mackerel at a small distance, and it needs support from critical experiments or observations indicating the sensory ability of a copepod in such a situation. If they do not possess this faculty the individual mackerel would be at no disadvantage as compared with a school in catching copepods.

Despite the lack of proof that schooling is an advantage in plankton feeding, there is strong indication that schooling is related to this method of feeding in the fact that schooling is so prevalent among species whose principal food is plankton. Furthermore, those schooling fishes (bluefish, tuna, bonito) which do not subsist primarily on plankton, feed instead mainly upon schooling fish, crustacea or cephalopods (menhaden, herring, sardines, euphausids, squid). Here the relation of predator to prey is essentially similar, i. e., a menhaden eluding one bluefish would be in the path of another, if the bluefish were in schools.

[7] To do this would require that each sample be sufficiently large to describe the size (or age) composition of a school. With limited resources it seemed better to take small samples from each of many catches (schools) rather than larger samples from fewer catches (schools). However, even these small samples might yield information if studied by statistical methods developed for quality control (Shewhart 1931).

SCHOOLING ACCORDING TO SIZE

A further feature of schooling, significant to the study of age composition, is the tendency of individuals of the same size to school together. Fish of the year, as far as we know, always school separately from the rest. Yearlings usually do, but, judging from samples, may sometimes join schools of adults, especially when the latter are predominately in their third year. The adults—third-year fish and upwards—seem not to separate themselves according to age or size in any sharply defined manner. Nevertheless there is often enough difference in the size distribution among samples from different catches to suggest some tendency of mackerel in a given size range to band together in schools distinct from those of another but overlapping range.

A physical explanation of the tendency for mackerel of different sizes to form separate schools is suggested by the activities of fish whose swimming was timed as they circled around the live car in which they were enclosed. Among several dozen mackerel thus observed together, there were two yearlings, while the remainder were of juvenile size. The juvenile mackerel schooled together traveling in circuits around the enclosure at the rate of 10 feet per second and keeping in the middle or upper levels. The two yearling mackerel traveled in company with each other around the enclosure at the rate of 19 feet per second, i. e., distinctly faster than the small ones, always keeping below the small ones, sometimes circling in the same direction, sometimes in the opposite.

There is a simple explanation for this difference in speed if the work performed by the mackerel is proportional to its weight and if it serves mainly to overcome friction between water and the surface of the fish.[8] Then large fish should move faster through the water because the weight of musculature increases as a cube of length and the area of the surface only as the square. So, with less surface friction to overcome per gram of muscle in large fish than in small the "cruising" speed of the former should exceed the latter for a given output of energy per unit weight of muscle.

[8] The work done in displacing water as the mackerel moves should increase in proportion with the weight, if stream-lining is equally efficient in all sizes. But since musculature is also proportional to the weight, the expenditure of the same amount of energy per unit weight at a given speed should accomplish the displacement of water for small as well as large fishes. Therefore, the work of displacing water should not differentially affect the speed of small as compare with large fishes.

Moreover, there probably are lower and upper limits on swimming speed imposed by the inherent capacity of the mackerel's physiological processes and these are reinforced or perhaps even narrowed by special features of the physiological and physical systems involved in the mackerel's swimming.

For instance, a lower limit on swimming speed is imposed by the mackerel's respiratory requirements. F. G. Hall (1930) found that the mackerel depends on swimming to produce sufficient flow of water past its gills for its respiration. This no doubt accounts for the generally observed facts (1) that mackerel are always swimming and never at rest and (2) that when the scope of swimming movements is restricted by putting them into small aquaria they soon die. Thus there must be a certain limit below which the swimming may not fall without disequilibrium between respiration and metabolic requirements. Although the existence of such a lower limit was established by Hall's experimental demonstration that respiration of the mackerel depended on swimming, he neither located this limit nor determined whether or not it varied as a function of size.

An upper limit would be imposed by the amount of energy the mackerel may expend in swimming without causing disequilibrium in its metabolic system. If resistance to passage of a mackerel through the water depends not only on its surface-volume ratio but also is a function of speed such that the resistance increases more than proportionally with speed, then the upper limit would tend to be sharpened. An inordinate amount of energy would be required to swim even moderately faster than that point at which the energy expended on swimming is currently replenished and exhaustion would quickly ensue.

Obviously the swimming rate is dependent on a number of physical and physiological interactions and my single set of observations on the swimming rates of the two sizes of mackerel is hardly sufficient to prove that the rate is dependent primarily on size. Indeed the considerable range in sizes of individual fish found in a single school argues against it.

With speed directly dependent on size one might expect the sorting, by sizes, to be fairly precise, for each size of fish would have a particular speed differing from that of other sizes, and only fish of one size could stay together. Actually, rather diverse sizes are found in the same school. This can occur if the smaller fish put forth relatively more exertion than the larger ones. This probably takes place

within a moderate size range. The size composition in a school perhaps is in a state of dynamic equilibrium where the tropistic tendency for aggregation causing uniform speed is opposed to the physical tendency toward different swimming speeds. Within certain size ranges the former tends to keep the individuals together, while the latter tends to separate them. This would produce the effect observed: that mackerel school together according to size but that schools contain individuals of enough diversity in sizes to provide extensive overlapping in the size range.

VERTICAL DISTRIBUTION

The American mackerel is generally regarded as a surface fish because practically all of the catch is taken at or near the sea surface. But at times some of them are on bottom for they are occasionally taken by trawlers in autumn and winter, and it cannot be assumed *a priori* that they may not also inhabit intermediate depths. It has already been indicated (p. 261) that in winter most of the mackerel probably inhabit mid-depths. What their lowermost limit is in summer must be determined by indirect means, for gear that is effective in mid-depths has yet to be developed.

Bigelow and Welsh (1925: 195) were of the opinion that "there is no reason to suppose that they ever descend more than a few fathoms during their [summer] stay, the supply of small crustaceans on which they feed being invariably richer above than below 50 fathoms depth in the Gulf of Maine." The vertical gradient of temperature in the summertime, in my opinion, affords additional reason to suppose that they stay in the upper levels and that the temperature influence would tend to keep them even nearer the surface than 50 fathoms, which, after all, is a considerable depth from the standpoint of fishermen using surface gear such as the purse seine.

Temperatures in the western part of the Gulf of Maine during July 1932 (fig. 4) prove the existence of a very pronounced thermocline in the region where mackerel were being caught at the time. At a typical station (A) the temperature was 16° C. (60° F.) at the surface and at 10 meters, but fell to 8° C. (46° F.) at 20 meters, and to 6° C. (42° F.) at 30 meters. Although other stations varied from this in detail, all had temperatures above 13° C. (55° F.) at the surface and all had temperatures below 7° C. (45° F.) at the 30-meter level. At most of them the temperature gradient crossed the 7° C. line near the 20-meter level.

While mackerel have been found in temperatures as low as 4° or 5° C., it is not likely that they would voluntarily enter or stay in water of temperatures lower than 7° or 8° C., for they are rarely found in surface waters as cold as this and only in the wintertime have they been found at any level in lower temperatures. Hence it is likely that the thermocline in the summertime forms a barrier or floor, constituting a lower limit of depth-range.

This floor may move up and down during the season; and its depth varies from place to place. It is formed by the warming of surface layers in the spring and summer and destroyed by their chilling in autumn. During the season when it is in existence, stormy periods lower it and calm warm periods raise it. It tends to be higher in inshore areas and lower in offshore areas; but vertical turbulence, which may attend currents or be induced by storms, modifies this rule. Judging from such few of the temperatures given by Bigelow (1926: 978–997) as are pertinent,[9] the 20-meter level shown in figure 4 is fairly typical for the western part of the Gulf of Maine in early summer. Later in the season and farther offshore the thermocline tends to be deeper, perhaps with 40 or 50 meters as the lower limit. The probability that the mackerel are located at levels too deep to show at the surface in offshore waters where the thermocline lies deeper may explain the dearth of catches (p. 297) from over the central deeps of the Gulf of Maine. However, it is also possible that they seldom occur at any depth in that area.

In summary, it appears that the vertical range of the mackerel is limited by temperature. During the height of the fishing season and throughout the major portion of the fishing area, they must be kept within 15 to 20 meters (8 to 11 fathoms) of the surface. At certain times and places they are free to descend to greater depths, but probably not much below 40 or 50 meters (22 to 27 fathoms) and usually not that deep.

From the standpoint of studying fluctuations in abundance and age composition, the additional question arises: Does their vertical distribution render all of the mackerel accessible to fishermen at all times during the summer, or only part of them

[9] Unfortunately, most of the serial temperatures did not include observations between the surface and 40–50 meters, hence, do not fix the position of the thermocline except to indicate that it was above rather than below 50 meters

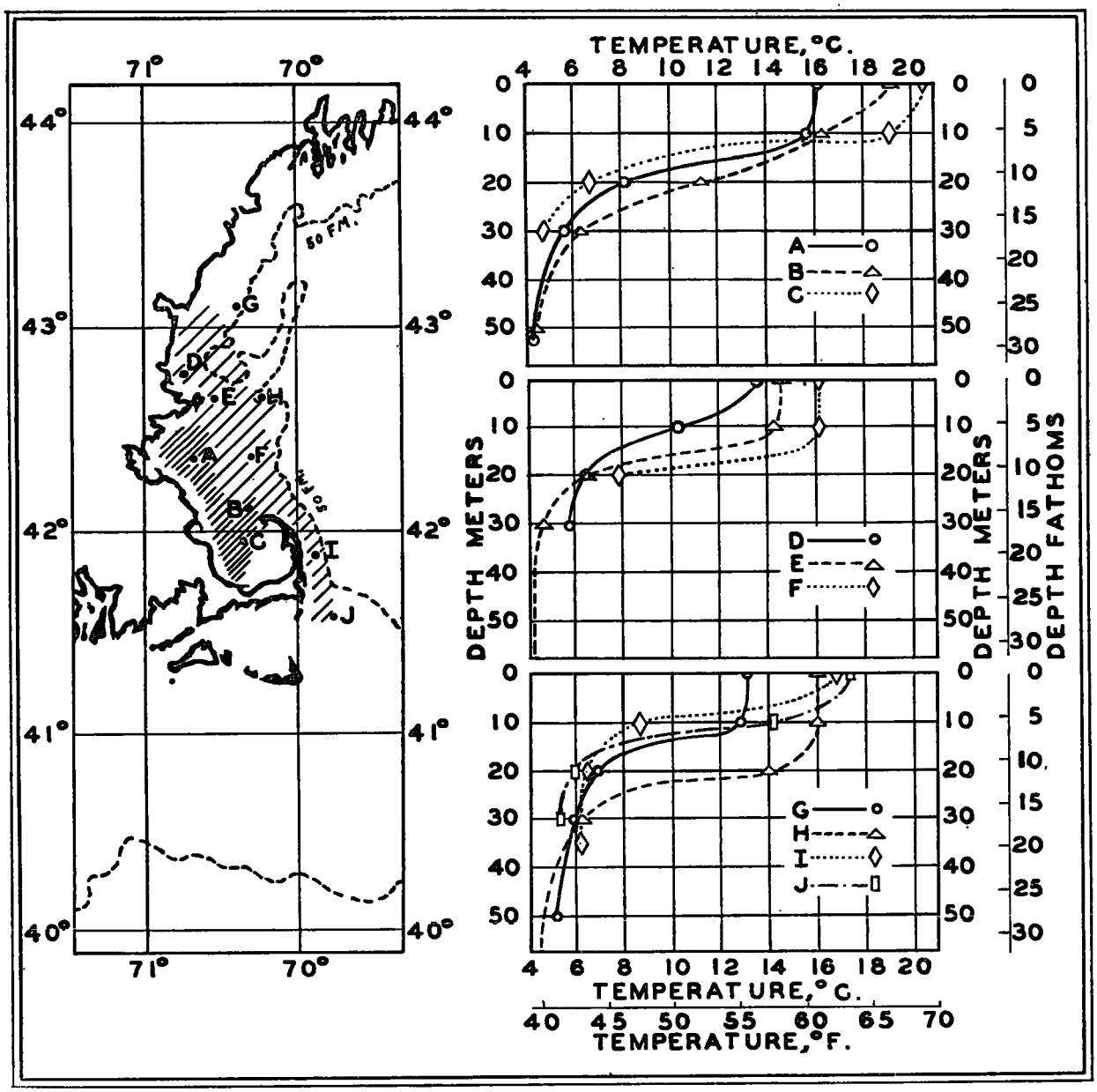


FIGURE 4.—Temperature gradients (vertical) in mackerel fishing waters. At the left are shown the areas where many catches were made (heavy shading), the areas where few were made (lighter shading), and the places where the temperatures were taken (lettered dots). On the right are the temperature gradient curves for each of the lettered positions. The catch data refer to the period, July 16–31, 1932, and the temperatures were taken July 22 and 23, 1932.

part of the time? Purse seines of ordinary size reach down to 20 fathoms, but their effectiveness depends not only on how deep they reach but also on how deep the schools can be seen and thus located before the seine is set.

In the daytime the schools are betrayed by a rippling of the water if they are at the surface, or by dark, shadowy, and sometimes reddish patches in the water if they are somewhat below the surface. How deep they may be detected depends on the height of the observer above the water, the quality of illumination, the roughness of the sea surface, the turbidity of the water, the keenness of vision and the alertness of the observer. Thus the depth at which they can be located is highly variable and not readily ascertained. It is reasonable to believe that

it seldom exceeds 10 fathoms and is usually less than that in the daytime.

On moonless nights, when the schools are visible as a luminescent patch in the water, it is probable that they can be seen at greater depths, because there is no interference from surface reflection. One instance illustrating the depth to which such luminescence is visible was reported by F. E. Firth in a letter written April 16, 1935, as follows: "Several, about 7, vessels went out Friday noon and returned Saturday P. M. without success." Captain Firth stated, "Saw a school firing deep in the water, made a set, pursed seine, got nothing, and the fish were still visible under the seine." He said, "the fish must have been down 25 fathoms, for his seine reaches down 22 fathoms. Water firing exceptionally well." This was, undoubtedly, an instance of remarkably good visibility. There is considerable variation in how well "the water fires"—to use fishermen's parlance—hence it cannot be expected that schools would always be seen at such great depths. It seems reasonable, however, to suppose that they can usually be seen down to a depth of 10 fathoms during night fishing.

Taking these considerations together, it is probable that the fishery is effective throughout the vertical range of the species only when favorable visibility coincides with a shoal thermocline. At other times, which must be frequent, a substantial portion of the mackerel population is inaccessible to the fishery on account of poor visibility, or because the fish are too deep, or combinations of these two impediments to the sighting of schools.

Although it is not possible to express the effect of vertical distribution quantitatively, it is obvious that the variations in the success of fishing may be modified considerably by the shifting up and down of the thermocline. When it is close to the surface, say within 10 fathoms, fishing should be good because nearly all of the population should be within vertical range of the fishing method. Unfortunately, serial temperature records are inadequate for determining the correlation between position of the thermocline and success of the fishery, but perhaps it is significant that fishing is less uniformly successful in spring and fall (when the thermocline is less well-defined) than in summer, and that even when fishermen sight mackerel in offshore waters where the thermocline is deeper it is only rarely that good catches are made there regularly over extended periods of time. The bathythermograph, developed after the close of this investigation, offers a new instrument for examining vertical temperature gradients speedily and in detail. Its application to this problem might demonstrate relationships that would be of high practical value in actual fishing operations as well as serviceable in biological research on population abundance and related subjects.

According to direct observations on mackerel in captivity during the present investigation and judging from fishermen's reports, the larger mackerel tend to swim deeper than the smaller ones. This is particularly true in mid and late summer. At such times fishermen often report that the schools of large individuals are deep and "hard to stop," meaning difficult to encompass with the seine. Accordingly, there may be a tendency toward catching a larger proportion of small mackerel than of large ones whenever and wherever the thermocline is relatively deep. This probably is the explanation of the "disappearance" of the large mackerel in the late summer of many seasons (p. 268). For these reasons it is probable that the fishermen's catch in the aggregate undersamples the larger mackerel and oversamples the smaller ones within the range of commercially desirable sizes.

This is one aspect of mackerel behavior among many others which may be grouped together under the heading of "availability." By this is meant all of the various elements in the behavior of the fish and of the fishermen which cause the catch to be out of proportion to the stock of fish. With pelagic fishes such as the mackerel, where the vertical as well as the horizontal extent of distribution affects the quantity caught, there is opportunity for availability to have a much more pronounced effect on the quantity caught than with nonpelagic fishes; and there is evidence that effects of availability extend also to the size categories caught.

It has become standard procedure in studying marine fish populations to use the commercial catch per unit of fishing effort as an estimate of abundance and the size composition or age composition of the commercial catch as an approximation of the size or age composition of the stock. This has worked well, notably with demersal fishes. With pelagic fishes the element of availability is so strong that it is safer to assume that the catch per unit of effort only indicates apparent abundance—not abundance itself, also that the distribution of sizes or ages in the catch registers something other than the size or

age distribution of the general stock in the sea. When these more limited assumptions are adopted, most of the established techniques for studying the dynamics of recruitment, natural mortality, and catch mortality of fish populations are no longer applicable. If they are applied, nonetheless, they are likely to lead to anomalous results.

In view of this, it appears likely that progress in understanding the dynamics of the mackerel population will be impeded until more is learned about the reactions of the mackerel to its environment and the quantitative effects these have on commercial catches as samples of the abundance and size composition of the mackerel stock. The discussions of this and the preceding sections are intended to point out some of the features which appear significant and some of the lines of study which might prove fruitful of results.

FOOD

According to Bigelow and Welsh (1925: 201), the American mackerel feeds chiefly on plankton, of which copepods form the dominant part, and among the copepods *Calanus finmarchicus* is by far the most important. In Europe the same is true in spring and early summer but in late summer and autumn the mackerel there turns its attention more to small fishes of various species.

Present observations, admittedly limited in extent, agree with those of Bigelow and Welsh. It is suggested, however, that the difference between the feeding habits of the mackerel in American waters and those in European waters in late summer may be more apparent than real, for we have found that the larger ones usually are not caught in quantity in late summer in American waters, and it may be that their search for larger food animals like euphausids and young fish leads them away from surface inshore waters at this time. Examination of stomach contents of such large mackerel as are occasionally caught offshore and in deeper water in late summer should be instructive on this point.

Whatever mackerel eat they are more successful in obtaining food after they have reached coastal waters in the spring than during their winter stay along the edge of the continental shelf. In April when mackerel first appear on the fishing grounds their fat content is very low and it increases markedly during ensuing months, according to analysis of the oil content of the flesh by Stansby and Lemon (1941: 10–11). Their values, supplemented by additional information communicated to me by Dr. Stansby, are summarized in table 2 While the data leave no doubt as to substantial fattening during the spring and early summer months, with the oil in the flesh increasing from about 4 percent in April to nearly 20 percent in August, the course of events during the remainder of the season is not clear. The values seem to fluctuate from sample to sample through a range from 6 to 19 percent. This, together with the wide variation between individuals within samples indicated by the minimum and maximum values, suggests that there is considerable difference in the success of individuals and groups of individuals either in feeding sufficiently or upon sufficiently nutritious food to provide an excess, over metabolic requirements, for fat storage. With some of the high oil content values attained as early as August, it also appears that feeding, on the whole, is usually better prior to August than after. However, the wide variation precludes any conclusion as to whether there is an average gain or loss of fat through the late summer and autumn months.

TABLE 2.—*Oil content of mackerel*

Date fish were caught	Number of fish analyzed	Oil content, percentage		
		Maximum	Minimum	Average
Apr. 18, 1935	13			3.9
Apr. 22, 1935	8	7.6	2.7	4.8
May 3, 1935	4			8.0
May 21, 1935	4			9.0
June 1, 1935	6			9.8
June 5, 1934				[1] 6.8
July 23, 1934	13	17.3	6.1	10.6
Aug. 13, 1934	7	25.6	10.6	17.5
Aug. 15, 1934	7	21.6	16.0	19.2
Sept. 11, 1934	20	11.4	2.0	6.5
Oct. 1, 1934	25	16.2	3.0	10.1
Oct. 20, 1934				[1] 15.7
Nov. 17, 1933	12	15.2	2.2	8.2
Nov. 17, 1934				[1] 19.5

[1] This value was derived from Stansby and Lemon's (1941) table 4, by taking the simple average of the percentage of oil content in the 31½- to 36½-inch, 36½- to 38-inch, and 39- to 42-inch size categories. The number of fish in the sample was not given.

MIGRATION OF ADULT MACKEREL

That mackerel migrate seasonally is generally accepted, but concerning the direction and extent of their travels there are two schools of thought—one that they migrate great distances from north to south when they leave the coast in the fall and back again in the spring; the other, that they sink and move directly out to deeper water in the fall and merely rise and move inshore in the spring. The controversy between the schools was lively in the latter part of the nineteenth century in connection with the dispute between the United States and

Canadian Governments concerning the right of United States fishermen to participate in the mackerel fisheries in Canadian waters (Goode, Geo. B., et al., 1884: 95). With both sides basing their argument on fragmentary data largely from testimony of unscientific observers, the question was in the realm of conjecture and remained there at least until 1908 (Kendall 1910: 293). Latterly, with more facts at hand, with respect to European as well as American mackerel, there was a decided leaning toward the school favoring the on-and-off-shore as against the north-and-south migration (Bigelow and Welsh 1925: 191).

With the more extensive, systematic, and detailed information available from the present studies, it now appears that neither school was wholly wrong or wholly right, for a critical comparison of all evidence points definitely toward the existence of a complex combination of the two (or three, if we include the vertical) sorts of movement. The general course of the migrations is diagrammatically charted in figures 5 and 6. Proof of the essential correctness of the routes shown requires consideration of their winter habitat, the existence of two migrating populations, a northern and a southern contingent, and various other relations which will be taken up in detail. But for the convenience of those who may not be interested in proofs and details, a summary of the migration will be given here.

SUMMARY DESCRIPTION OF MIGRATION

Although both the northern and the southern contingents are supposed to spend the winter in the zone of warm water, some thirty to one hundred miles out to sea along the continental edge from Virginia to Nova Scotia, it is probable that the members of the southern contingent tend to be at the southerly end of this zone, and those of the northerly contingent at the northerly end.

The southern contingent first appears in the surface waters overlying the continental shelf somewhere between Cape Hatteras and the offing of Delaware Bay, and usually in the early days of April. Though at first some thirty to fifty miles offshore, they soon come closer inshore occupying the inner third or half of the continental shelf which is about fifty miles broad at Delaware Bay. From here they move northward and eastward at a rate not faster than the progressive northerly warming of the surface water and reach the offing of southern New England during the month of May. During the northerly journey they are joined by additional schools moving in from the edge of the continental shelf in wavelike incursions. Although the southern contingent always tarries a month or more in the vicinity of southern New England, toward the end of June or early in July its members make their way around Nantucket Shoals and reach the Gulf of Maine where they make their summer sojourn.

The northern contingent makes its appearance during the latter half of May forming a wave advancing toward the coast along a broad front, perhaps from Hudsonian Channel eastward. The western end of this wave strikes the southern coast of New England, the middle portion, southern Nova Scotia and the eastern, the more easterly portions of Nova Scotia. Once inshore, the members of this contingent migrate along shore. Those that strike the coast of southern New England mix temporarily with the southern contingent among which they are detectable by their different (usually larger) sizes. But after staying only a week or two they separate from the southern contingent and toward the end of May some filter into Massachusetts Bay, but the major portion are next to be found on the Nova Scotian coast reaching there during the early days of June about the same time as those that approached that coast directly. During June, the run is heavy along the entire length of the Nova Scotian coast, Cape Breton, and eastern portions of the Gulf of St. Lawrence. During this June run there are perhaps additional minor waves of mackerel coming shoreward from the outer edge of the Nova Scotian shelf if any have wintered in the more chilly waters of this region (p. 261). Most of the northern contingent probably summers in the Gulf of St. Lawrence though part may remain along the coasts of Maine, Nova Scotia, and Capte Breton Island.

In withdrawing from the coastal areas in the fall, the movements of the two contingents, for the most part, are simply the reverse of their approach in the spring. The southern contingent in retiring from the Gulf of Maine goes southeastward past Cape Cod and in some years then trends westerly off No Man's Land and Block Island. This usually take place in September or October. About the same time, though sometimes earlier and sometimes later, the northern contingent begins retiring from Canadian waters. In doing so, a large portion, if not all, passes through the Gulf of Maine providing the basis for the late fall fishery off Cape Anne in October, November,

and December. They, too, leave the Gulf of Maine by going toward the offing of Cape Cod, but have never been observed southerly or westerly of that area. During the fall migration, as during the spring migration, there is a brief period when the two contingents are mixed. The fall withdrawal differs from the spring approach mainly by the mixing of the two contingents north rather than south of Nantucket Shoals; the disappearance of each contingent while still well north of the points at which they first appeared in the spring; and the occupation by the northern contingent of the western portion of the Gulf of Maine to a greater extent and for a longer period in the fall than in the spring.

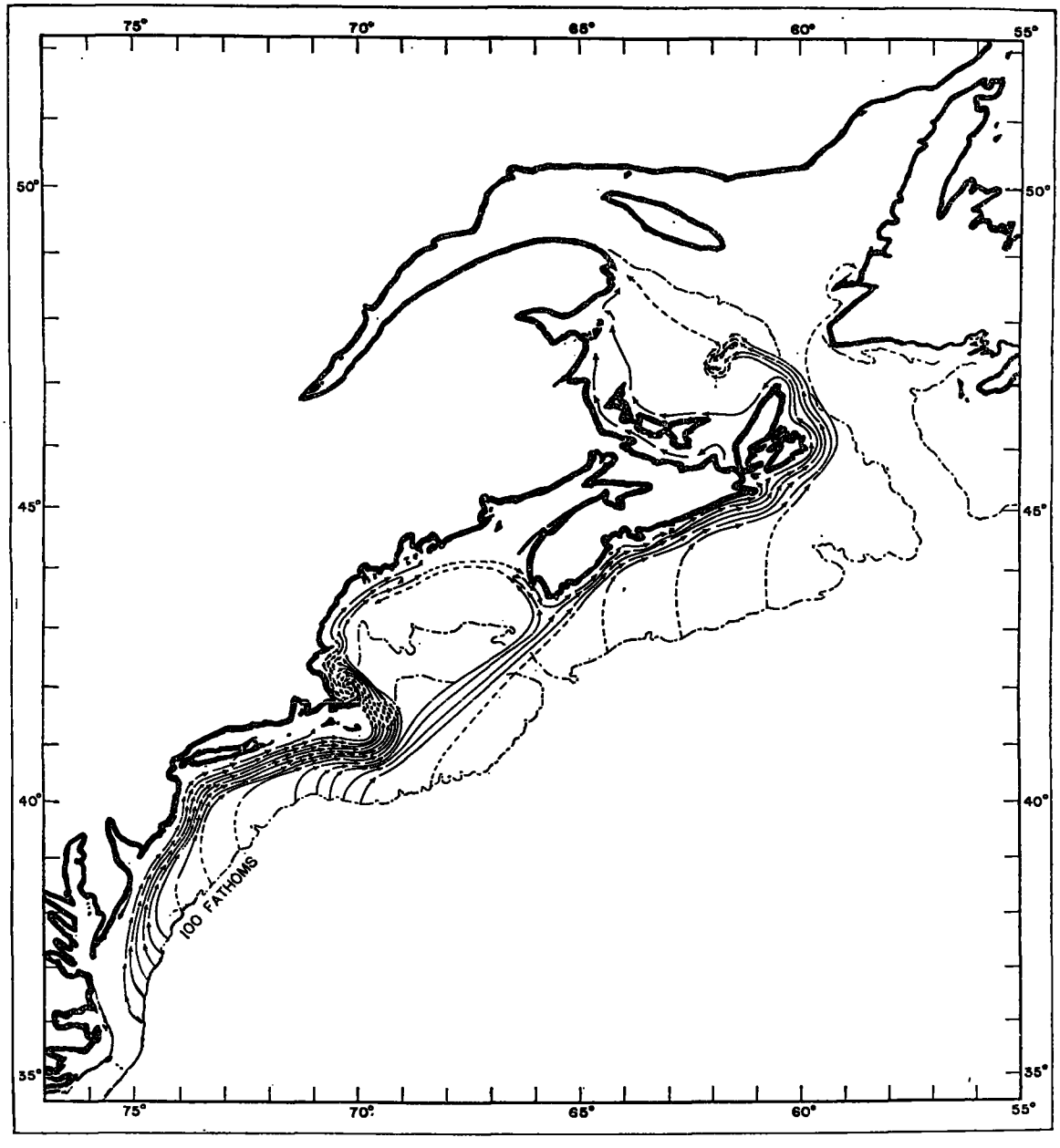


FIGURE 5.—Diagrammatic representation of the spring migration. The number of arrowshafts is roughly proportional to the relative number of mackerel believed to traverse the several localities. The number of arrowheads is roughly proportional to the relative amount of commercial catch taken in the several areas. Lines of dashes indicate weak evidence as to the origin or route of migration.

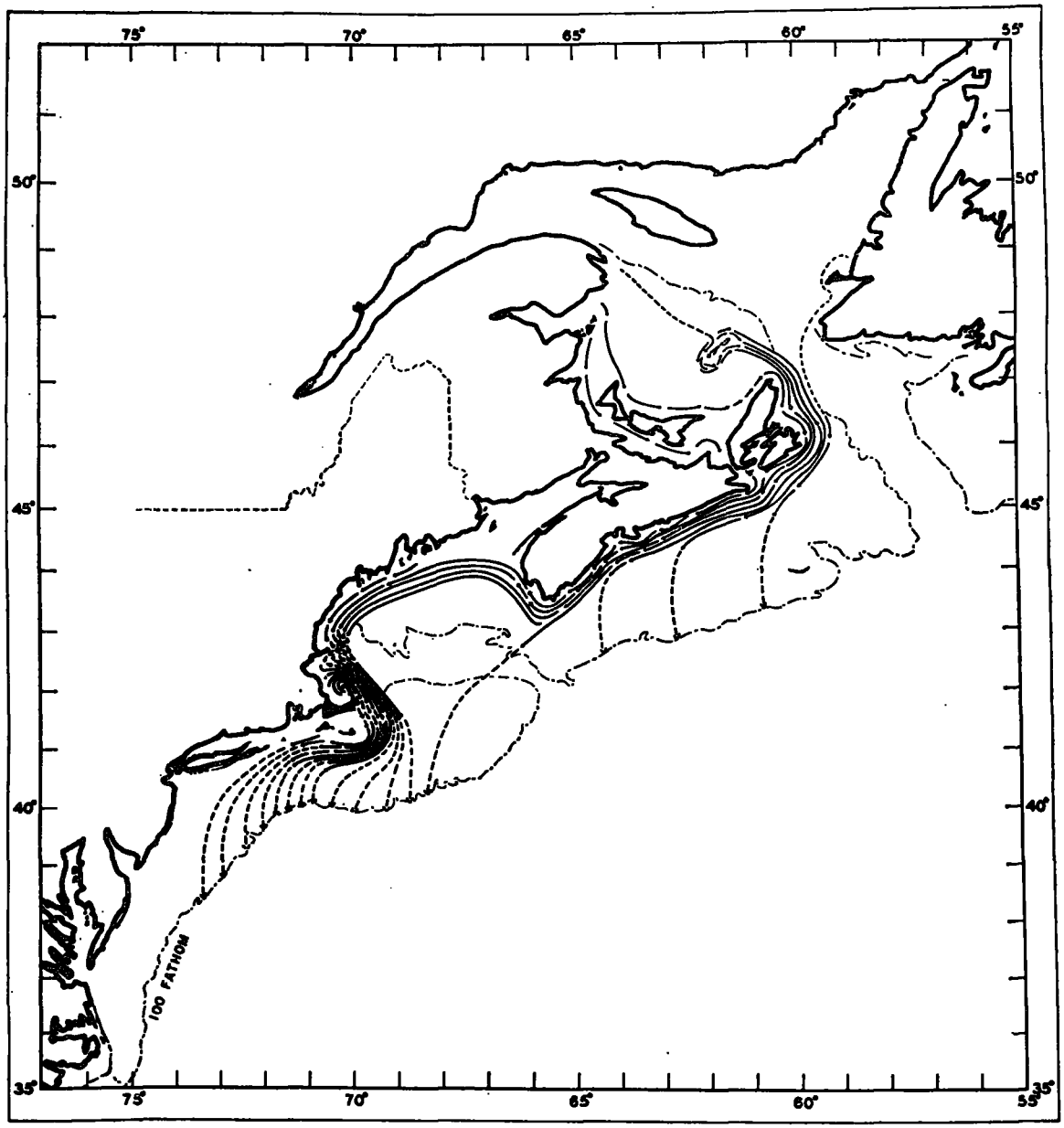


FIGURE 6.—Diagrammatic representation of the fall migration. The number of arrowshafts is roughly proportional to the relative numbers of mackerel believed to transverse the several localities. The number of arrowheads is roughly proportional to the relatve amount of commercial catch taken in the several areas. Lines of dashes indicate weak evidence as to the route or destination of migration.

The supporting evidence rests almost solely on the observed size composition of the mackerel population at various times and places, together with the time sequence of the appearance of the population—or certain portions of it—at the various points along the coast. This evidence, although indirect, has a notable advantage over the more direct method of tagging. It enables one to deal with a much larger portion of the population and to obtain a much more definite estimate of the relative numbers of individuals involved in the movements (i. e., distinguish mass-movements from stragglings) than can be

gained from the relatively small numbers usually tagged. Nevertheless, tagging experiments were done, which furnish confirmation (p. 307).[10]

DISTINCTION BETWEEN NORTHERN AND SOUTHERN CONTINGENTS

To account for the several phenomena observed in the migration study it has been necessary to recognize the existence of two subdivisions of the mackerel population which differ in their migrating habits, and which it is convenient to designate as southern and northern contingents. It is not necessarily implied that these are genetically distinct races of the species such as were believed to exist in European waters by Garstang (1898: 235–295) on the basis of differences in morphological characters. For the purpose of discussing the migrations it is preferable to regard the two contingents as subdivisions of more or less stable nature enduring through several seasons, but not necessarily from one generation to another.

The phenomena that indicated two subdivisions or contingents within the population along the North American coast are (1) the prevailing dissimilarity in size composition of the spring population along the Nova Scotian coast ("Cape Shore" in the parlance of mackerel fishermen) from the spring and summer population along the New England and Middle Atlantic coasts; and (2) the pronounced but transient alteration of sizes in the population off southern New England that takes place each year, usually in late May. The nature of these phenomena will be illustrated by the data of 1927, the relation between them will be demonstrated with the data of 1932 and finally their persistence or annual recurrence during the period of this investigation will be shown.

Because the size composition of the mackerel population was simple in 1927, the data of that year afford a favorable opportunity to illustrate both of the phenomena under consideration. In the population along New England and Middle Atlantic States, which will be termed "southern contingent," the 1923 class was so predominant that the length-frequency curves of that season were almost always characterized by a nearly symmetrical simple curve with a mode at 39 centimeters (two lowermost and three uppermost panels of fig. 7). The population along the Nova Scotian coast, which will be termed "northern contingent," on the other hand was dominated by the 1921 class as is evident from its simple mode at 41 centimeters (broken-line curve in middle panel of figure 7).[11] But the composition of the population off southern New England was altered during a brief period, so that frequency distributions of samples in the last half of May and again in the first half of June were essentially bimodal, with modes at 39 and 41 centimeters (the third and fourth panels from bottom in fig. 7). The simplest explanation of this altered size composition is that both northern and southern contingents for a time occupied the same area, were caught indiscriminately by the fishermen, and occurred in a mixture in the samples drawn from the catch. Since the alteration in size composition off southern New England (May 16–31) antedated the appearance of the larger fish along the Nova Scotian coast (June 1–15) it appears that the northern contingent in its migration first passed along the southern New England coast, mixed temporarily with the southern contingent already there, and then went on to the Nova Scotian coast, leaving the southern contingent behind.

This explanation may be tested to see whether it is fully in accord with the facts by combining the northern contingent as sampled off Nova Scotia with the southern contingent as sampled off southern New England before and after the mixing period, and comparing the resultant "synthetic" curve with the altered distribution found off southern New England, which may be termed the "mixed population." For purposes of this test the data of 1932 are more suitable than those of other years because fishing took place both off Nova Scotia and off southern New England during the periods that are critical to this experimental synthesis and hence both populations were well-sampled in that year.[12]

If the data of May and June of 1932 be summarized in reasonably short time intervals and by subareas as in figure 8, it is obvious that the southern contingent of that year was characterized by a dominant mode at 43 centimeters and a subdominant

[10] In using this order of presentation we are following the procedure actually used in arriving at the present results. Preliminary examination of tagging returns originally secured were unintelligible, and the data were laid aside for some years. It was not until the size composition study was completed that the tagging evidence was again consulted and found intelligible in the light of the hypothesis built up from the evidence gained by sampling the population.

[11] The irregularity of this curve is due to the scanty sampling afforded by the two catches from this area in 1927 and does not indicate multimodality or other complexities.

[12] In many seasons the fleet fishes either almost wholly off southern New England or almost wholly off Nova Scotia at this time so that sampling usually is deficient in either one place or the other.

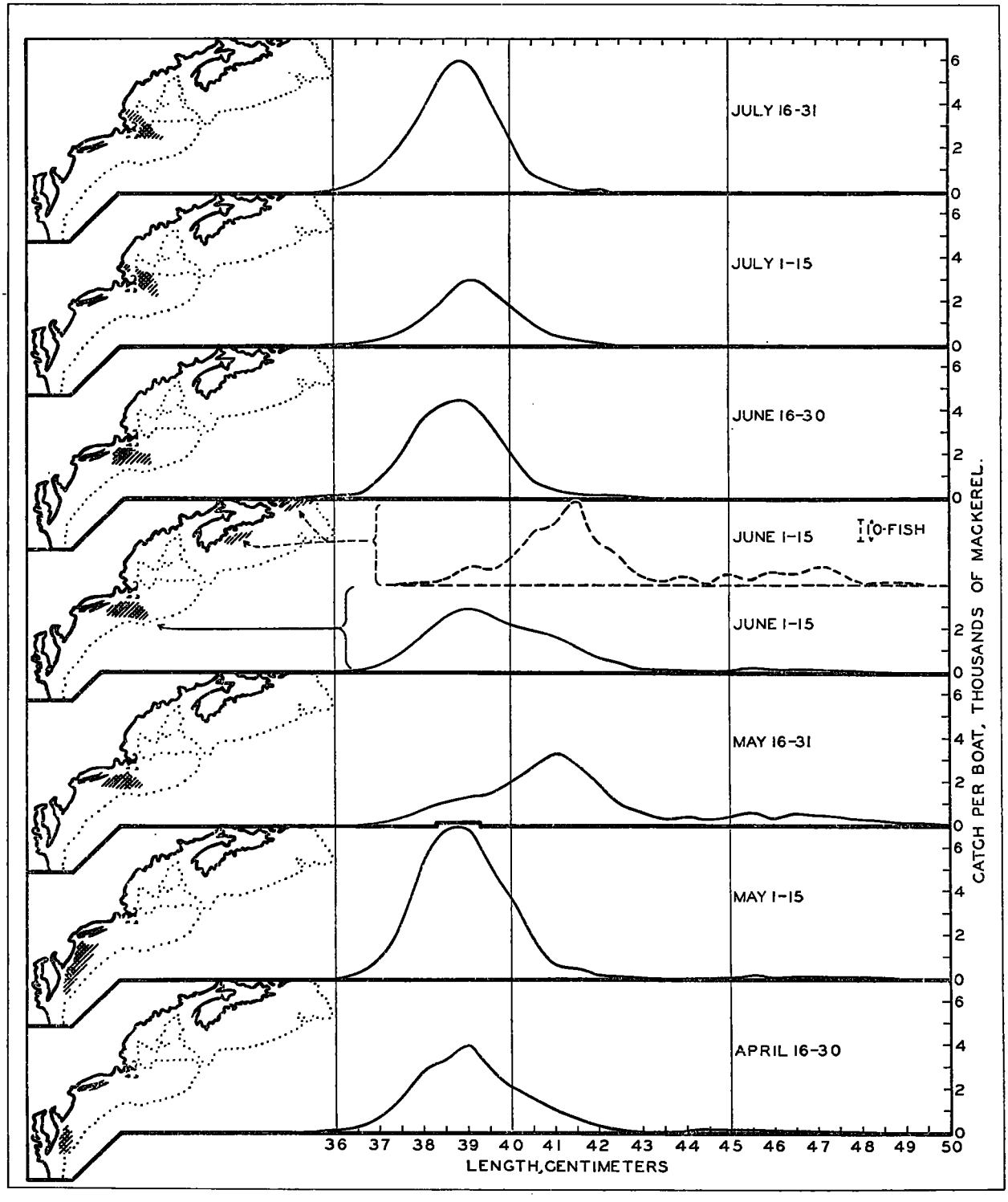
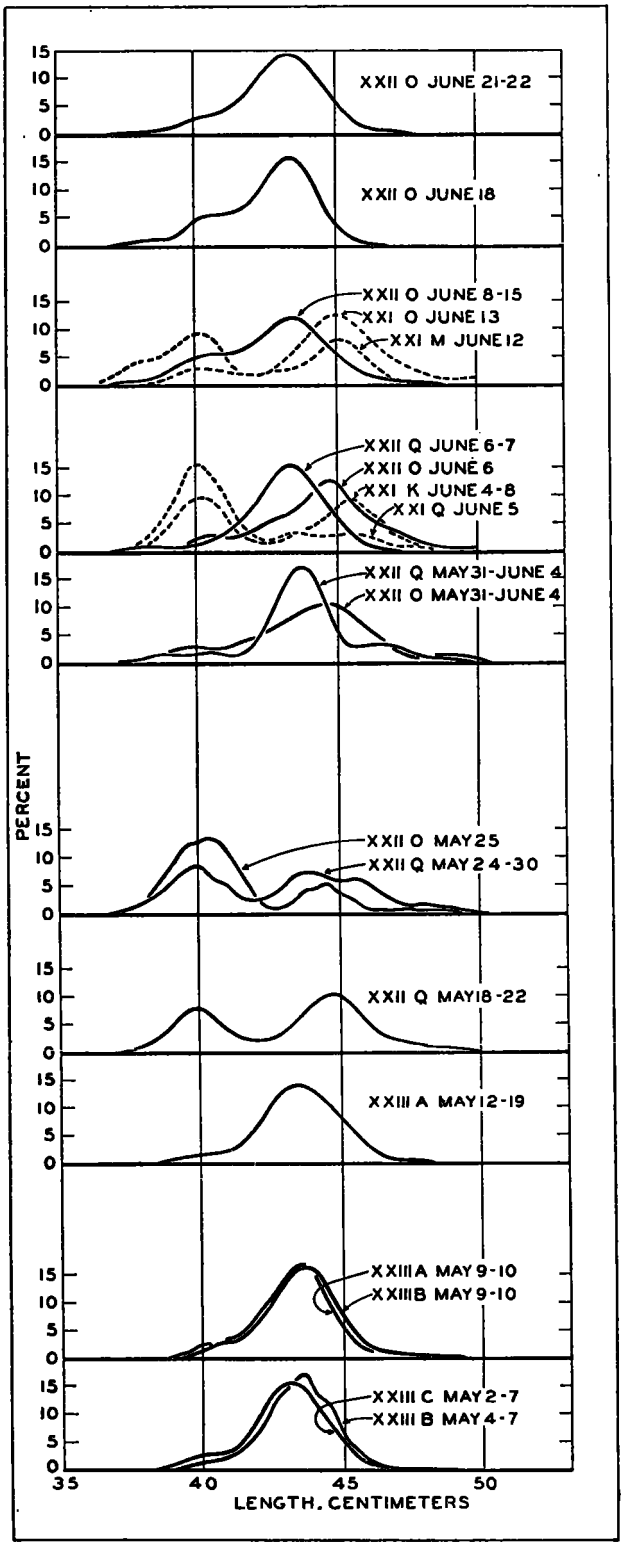


FIGURE 7.—Changes in the size composition of the mackerel in purse-seine catches in the spring of 1927. The areas under the curves are proportional to the catch per unit of effort except for the broken curve of samples from the coast of Nova Scotia, June 1–15. The shaded areas in the chart insets at the left indicate the localities of fishing during each half month.



mode at 40 centimeters and the northern contingent by nearly equal modes at 40 centimeters and at 45 or 46 centimeters. With these criteria the samples are readily classified into three groups as in tables 3, 4, and 5 representing northern, southern, and mixed population, respectively. Taking as ingredients length distributions of the northern and southern contingents smoothed as shown in figure 9, it was found by successive trials that combined in the ratio of 68 northern to 32 southern they formed a curve approximating the mixed population. Graphic indication of goodness of fit is given in the middle panel of figure 9. The chi-square test (Fisher 1932: 80) also indicates a tolerably good fit, there being as high as 1 chance in 10 that the difference might be exceeded owing to random causes alone.[13]

Hence the size composition of the so-called mixed population is consistent with the hypothesis that the ingredients of the mixture were indeed of the northern and southern contingents as here defined. The size composition also indicated that during the period of mixing the northern contingent outnumbered the southern by approximately 2 to 1.

The fact that northern contingent mackerel appeared on May 18 in southern New England waters before their appearance on June 4 in Nova Scotian waters suggests that on separating out of the mixture off southern New England, this group went to the coast of Nova Scotia. Detailed examination of the curves of frequency distribution are still more suggestive of such a movement, for in

[13] That portion of the curve above 41.5 centimeters fits much better (P=0.30) than the portion below (P=0.01). The poorness of fit below 41.5 centimeters may be attributed to sampling deficiencies rather than to significant differences in the populations concerned because a large part of the contribution to chi-square is from the excess at 39.5 and deficiency at 40.5 and 41.0 centimeters in the observed mixture and these in turn result mainly from the frequency of area XXII O, May 31 to June 4 which dominates the grouped mixture. If the five components in the mixture be recombined after giving equal weight to each (percentage frequencies) the above-mentioned excess and deficiencies are very much reduced, showing that the distribution of sampling during the period of mixing has somewhat altered the shape of this portion of the curve. Although this might be overcome by a system of weighting, this was not done because it would have interfered with the chi-square test.

FIGURE 8.—Size composition of mackerel in purse-seine catches in the spring of 1932. The spaces between base lines are approximately proportional to the time between weighted mean dates of groups of samples included in the distribution plotted on the respective base lines. Samples pertaining to each area and period were simply grouped by direct addition without weighting, smoothed by a moving average of three, and reduced to equal areas by converting to percentages.

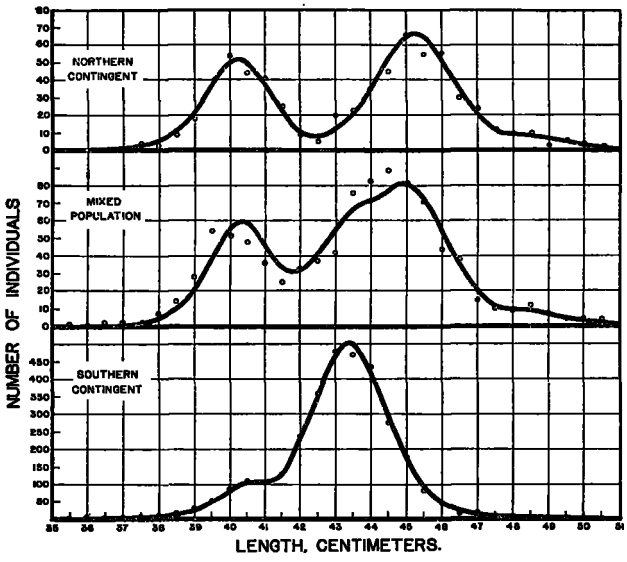


FIGURE 9.—Relationship of northern and southern contingents to the "mixed" population. In the upper and lower panels the circles represent observed numbers, the lines represent the graphically smoothed curves. In the middle panel the circles represent observed numbers, the line represents the combination of northern and southern contingents in the ratio of 68 to 32. Data were derived from tables 3 to 5.

TABLE 3.—*Size composition of the northern contingent in June 1932*

[Letters at head of columns specify subareas (fig. 1)]

Length in centimeters	Area XXI				Total
	K	Q	O	M	
	June 4–8	June 5	June 13	June 12	
	Number	*Number*	*Number*	*Number*	*Number*
37.5	1		1	2	4
38.0		1		2	3
38.5	7			2	9
39.0	11	3	2	2	18
39.5	21	7	5	4	37
40.0	38	5	7	4	54
40.5	25	8	6	5	44
41.0	30	2	4	2	38
41.5	15	3	6	1	25
42.0	5	1	3		9
42.5	1		2	2	5
43.0	8	1	10	1	20
43.5	6	3	11	1	21
44.0	12		20	2	34
44.5	16		27	2	45
45.0	28	3	30	5	66
45.5	27		25	3	55
46.0	27	2	21	3	53
46.5	16		13	1	30
47.0	12	1	11		24
47.5	4		6		10
48.0	3		6		9
48.5	6		2	1	9
49.0	3				3
49.5	2		2		4
50.0			3		3
50.5			2		2
52.0	1				1
Total	325	40	225	45	635

TABLE 4.—*Size composition of the southern contingent in May and June 1932*

[Letters at head of columns specify subareas (fig. 1)]

Length in centimeters	Area XXIII					Area XXII					Total
	C	B		A		Q		O			
	May 2–7	May 4–7	May 9–10	May 9–10	May 12–19	May 31–June 4	June 6–7	June 8–15	June 16–20	June 21–22 [1]	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
35.5	1										1
36.0								3			3
36.5										1	1
37.0	2							1	1		4
37.5			1					3		2	6
38.0	1	1					2	2	1	2	9
38.5	2				1	1	1	7	2		14
39.0	6					2	2	17	1	2	30
39.5	10	2	1	1	4	1		24		6	49
40.0	20	3	6	2	2	1	3	31	7	10	85
40.5	17	6	8	3	4	2	3	42	9	12	106
41.0	21	4	12	1	7	2	5	34	6	11	103
41.5	30	10	9	4	6		8	34	7	20	128
42.0	62	20	26	6	18	2	18	46	12	25	235
42.5	102	26	37	9	28	8	16	71	12	48	357
43.0	131	52	46	11	38	13	36	77	25	49	478
43.5	96	39	73	15	38	15	27	91	23	52	469
44.0	87	46	54	14	35	21	28	73	19	48	425
44.5	62	26	43	7	28	10	13	54	8	25	276
45.0	27	20	26	3	22	3	12	34	6	23	176
45.5	16	6	10	2	12	2	5	21		6	80
46.0	5	4	6	1	9	3	2	11		2	43
46.5	2		2		2	3		4	1	2	16
47.0	2	1	3	1	1	3	1	5		1	18
47.5	1				2	1		3		1	8
48.0	1	2	2		1	1	1				8
48.5	1	1	1			1		1			5
49.0			1							2	3
49.5			1		1		1				3
50.0					1		1				2
50.5								1			1
Total	705	269	368	80	260	95	185	690	140	350	3,142

[1] Includes 20 from H.

TABLE 5.—*Size composition of the mixed population in May and June 1932*

[Letters at head of columns specify subareas (fig. 1)]

Length in centimeters	Area XXII					Total
	Q		O			
	May 18–22	May 24–30	May 25	May 31–June 4	June 6	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
35.5				1		1
36.0		1				1
36.5	1		1			2
37.0				2		2
37.5		1		1		2
38.0	1	3	2	1		7
38.5	3	6	2	3		14
39.0	6	7	9	6		28
39.5	10	16	10	18		54
40.0	13	14	11	14	1	53
40.5	9	15	11	10	3	48
41.0	3	4	13	15	1	36
41.5	3	6	3	12	1	25
42.0	2	3	2	23	3	33
42.5	3	4		27	3	37
43.0	4	7	1	24	6	42
43.5	7	14	2	51	2	76
44.0	13	14	6	42	8	83
44.5	14	9	2	55	9	89
45.0	15	11	5	41	9	81
45.5	11	9	1	46	4	71
46.0	6	10		22	6	44
46.5	4	8		25	1	38
47.0	3	1	1	7	3	15
47.5	2	2		4	2	10
48.0	1	2	1	4	1	9
48.5	2	3		7		12
49.0		1		5	1	7
49.5		1	1	2		4
50.0				4		4
50.5				3	1	4
Total	136	172	84	475	65	932

area XXII–Q,[14] May 24 to 30, there is a prominence in the distribution at 45.5 centimeters which is comparable to a prominence at the same position in the Nova Scotian samples of area XXI–K, June 4 to 8. By May 31 the prominence in southern New England is more marked in the vicinity of 45.0 centimeters which may be compared to the similar prominence in the Nova Scotian material of area XXI–O and area XXI–N, June 12 and 13. In other words, there is a lag of about 10 days between the appearance of certain categories of mackerel in southern New England and the appearance of the same fish in Nova Scotian waters. This corresponds to the average lag between the first appearance of northern contingent mackerel in southern New England and first appearance in quantity of mackerel in Nova Scotia in the various years between 1926 and 1932 (p. 270).

To determine whether or not the change in size composition just noted for 1927 and 1932, and attributed to the existence of a northern contingent distinct from a southern contingent, is a regular event recurring year after year among the mackerel caught off the United States coast during the spring, each year's length-frequency distributions, grouped by statistical subareas and by relatively short periods of time, similar to the groupings used for 1932 in tables 4 and 5 and figure 8 were examined. On the basis of position and dominance of modes it was possible to distinguish distributions obviously representing a mixed population intermediate between the southern contingent (as represented in distributions displaying a stable combination of modes consistently through April, part of May and

[14] See fig. 1 for delineations of areas.

TABLE 6.—*Statistical areas and time periods characterized by mixed population in May and June in the years 1926 to 1935*

[Unless otherwise indicated only purse-seine-caught mackerel are included]

Statistical area	Time period	Number of mackerel
	1926	
XXIII B, XXII O, Q	June 14–15	100
XXII P, R	May 28–29 (caught by gill net)	120
XXII Q, R	June 1, 12 (caught by gill net)	180
XXII P	June 1, 11, 15 (caught by gill net)	160
XXII D	June 11, 14, 15 (caught by gill net)	140
XXII E	June 1–15 (caught by gill net)	1,159
Total		1,859
	1927	
XXII Q, S	May 16–20	240
XXII, P, Q, S XXIII A	May 21–25	990
XXII O, P, Q	May 26–31	670
XXII O, P, Q, S	June 1–5	1,240
Total		3,140
	1928	
XXIII A, XXII Q	May 25	160
XXII P, Q, R	May 26–31	589
XXII P, Q	June 1–2	220
Total		969
	1929	
XXII Q	June 6–7	80
XXII E	June 12–17	187
XXII D	June 15	32
Total		299
	1930	
XXII S, Q	May 19	40
XXII Q, R	May 20	116
XXII Q	May 21–26	250
Total		406
	1931	
XXII Q	May 17–31	460
XXII S	May 22–23	102
XXII O	June 1	40
Total		602
	1932	
XXII Q	May 18–31	311
XXII O	May 25 to June 6	625
Total		936
	1933	
XXII Q	May 18–25	220
	1934	
XXIII A	May 14–17	740
XXII Q, R, S	May 17–19	792
XXII O, Q	May 22 to June 2	3,841
Total		4,373
	1935	
XXII Q	May 20 to June 10	3,805

June, and through July) and the northern contingent (as represented in distributions from purse-seine catches off the coast of Nova Scotia). The statistical subareas and periods of time characterized by the mixed population type of distribution are listed in table 6 together with the number of mackerel contained in the samples available from each. These samples were pooled and their length-frequency distributions summarized in table 7. The remainder of the May and June samples from areas XXII and XXIII representing the southern contingent, are similarly given in table 8 and the Nova Scotian samples (area XXI) representing the northern contingent are given in table 9. The three series, converted to percentages, are shown in figure 10. In this figure the curves have been drawn through the unsmoothed percentage-frequency values. Where they are markedly irregular it is due to the small numbers involved as can be seen by reference to tables 7, 8, and 9.

TABLE 7.—*Length frequencies, by half-centimeter classes, of mackerel in the mixed population, as represented by samples from the statistical subareas and dates listed in table 6*

Length in centimeters	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935
27.0	-----	-----	-----	-----	-----	-----	-----	-----	-----	4
27.5	-----	-----	-----	-----	-----	-----	-----	-----	-----	1
28.0	-----	-----	-----	-----	-----	-----	-----	-----	-----	2
31.0	-----	-----	-----	-----	-----	-----	1	1	1	1
31.5	-----	-----	-----	-----	-----	-----	-----	1	3	29
32.0	-----	-----	-----	-----	-----	-----	2	4	3	50
32.5	-----	-----	-----	1	-----	-----	-----	2	5	101
33.0	-----	-----	-----	-----	-----	-----	-----	12	8	134
33.5	-----	-----	-----	-----	-----	-----	1	9	6	117
34.0	-----	1	-----	-----	1	-----	-----	11	16	115
34.5	-----	-----	-----	-----	-----	1	-----	5	43	73
35.0	-----	-----	-----	-----	-----	1	-----	14	104	36
35.5	1	-----	-----	-----	-----	-----	1	12	202	33
36.0	4	-----	-----	2	1	-----	1	2	329	68
36.5	17	2	-----	-----	-----	1	2	8	374	137
37.0	34	19	-----	1	2	3	2	2	358	275
37.5	45	55	1	-----	-----	3	2	2	220	382
38.0	71	118	4	-----	1	5	7	1	142	498
38.5	84	184	20	-----	1	29	14	3	69	448
39.0	82	219	42	1	1	25	28	-----	52	296
39.5	110	246	77	-----	1	42	54	2	31	194
40.0	127	309	89	7	1	34	53	3	49	104
40.5	166	384	129	8	5	14	48	3	80	43
41.0	166	423	122	21	4	8	36	5	89	44
41.5	139	341	121	37	10	20	25	8	128	34
42.0	108	215	81	37	14	36	33	3	103	46
42.5	67	114	62	45	21	39	37	5	125	38
43.0	41	62	48	52	28	44	42	8	156	47
43.5	29	39	31	27	47	41	76	10	202	80
44.0	39	30	16	15	47	56	83	10	262	68
44.5	47	29	13	12	54	53	89	7	263	63
45.0	75	39	14	4	42	39	81	16	260	62
45.5	76	65	10	10	32	29	71	20	240	70
46.0	76	31	8	3	16	28	44	16	148	44
46.5	85	51	17	2	12	11	38	7	131	31
47.0	62	44	16	4	11	13	15	3	68	14
47.5	25	38	13	1	18	4	10	2	39	6
48.0	38	30	7	2	13	6	9	1	29	7
48.5	14	22	10	2	8	8	12	-----	10	7
49.0	20	10	11	2	11	2	7	2	9	1
49.5	5	9	1	3	2	3	4	-----	10	2
50.0	2	5	2	-----	2	3	4	-----	3	-----
50.5	3	4	2	-----	-----	1	4	-----	2	-----
51.0	-----	1	2	-----	-----	-----	-----	-----	1	-----
51.5	1	1	-----	-----	-----	-----	-----	-----	-----	-----
Total	1,859	3,140	969	299	406	602	936	220	4,373	3,805

TABLE 8.—*Length frequencies, by half-centimeter classes, of mackerel in the southern contingent as represented by all May and June samples from areas XXII and XXIII other than those included in table 7*

Length in centimeters	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935
18.0	-----	-----	-----	-----	-----	1	-----	-----	-----	-----
19.0	-----	-----	-----	-----	-----	2	-----	-----	-----	-----
19.5	-----	-----	-----	5	-----	8	-----	-----	-----	-----
20.0	-----	-----	-----	7	-----	9	-----	-----	-----	-----
20.5	-----	-----	1	9	-----	23	-----	-----	-----	-----
21.0	-----	-----	-----	3	-----	13	-----	-----	-----	-----
21.5	-----	-----	2	7	-----	25	-----	-----	-----	-----
22.0	-----	-----	6	8	-----	15	-----	-----	-----	-----
22.5	-----	-----	7	18	-----	10	1	-----	-----	-----
23.0	-----	-----	13	24	-----	5	2	-----	-----	-----
23.5	-----	-----	12	42	2	1	1	-----	-----	-----
24.0	-----	-----	15	51	5	3	2	-----	-----	-----
24.5	-----	-----	7	49	7	-----	2	-----	-----	-----
25.0	-----	-----	7	47	13	-----	12	-----	-----	1
25.5	-----	-----	4	36	27	1	18	-----	3	1
26.0	-----	-----	4	39	16	-----	49	-----	1	1
26.5	-----	-----	-----	27	20	-----	51	-----	1	1
27.0	-----	-----	3	29	5	1	99	-----	-----	2
27.5	-----	1	-----	29	11	1	117	-----	1	3
28.0	-----	-----	-----	15	7	3	179	-----	-----	2
28.5	-----	1	-----	15	3	6	230	-----	1	2
29.0	1	1	-----	22	6	2	289	1	1	1
29.5	-----	1	-----	39	2	2	258	5	3	-----
30.0	-----	-----	-----	51	3	5	300	10	10	-----
30.5	-----	-----	-----	27	2	-----	281	37	17	-----
31.0	-----	-----	-----	18	4	-----	229	71	24	4
31.5	-----	-----	-----	4	2	1	191	183	57	10
32.0	-----	-----	-----	1	5	1	113	271	102	74
32.5	-----	-----	-----	2	13	2	64	346	119	143
33.0	5	-----	-----	3	35	4	33	351	89	271
33.5	7	-----	-----	7	106	11	9	280	94	306
34.0	10	-----	-----	16	326	27	7	222	105	308
34.5	16	1	-----	19	526	46	4	174	148	220
35.0	26	8	-----	41	663	83	2	101	338	145
35.5	53	5	-----	50	631	69	2	55	617	49
36.0	170	26	1	58	370	65	3	49	781	37
36.5	379	57	1	48	202	49	1	22	802	56
37.0	727	212	9	36	73	48	4	10	584	136
37.5	1,078	552	23	21	45	88	6	8	313	285
38.0	1,141	1,085	113	21	31	180	9	12	186	539
38.5	887	1,428	340	8	21	228	15	5	66	663
39.0	562	1,520	829	29	11	269	32	21	47	724
39.5	284	1,216	1,247	92	17	256	53	21	39	499
40.0	156	816	1,410	265	30	164	89	33	69	309
40.5	124	420	1,154	557	64	150	108	52	79	149
41.0	72	225	724	923	137	187	105	68	129	104
41.5	65	129	414	977	256	312	133	113	177	96
42.0	42	66	163	1,001	400	538	238	147	212	154
42.5	30	34	78	682	374	673	361	230	316	168
43.0	30	23	38	429	385	770	485	301	423	295
43.5	23	15	21	183	313	638	478	298	539	353
44.0	34	20	17	98	189	483	425	234	558	451
44.5	37	14	10	44	119	294	281	198	449	417
45.0	54	27	13	30	76	165	179	135	335	351
45.5	67	40	17	20	37	96	81	59	185	270
46.0	63	33	17	27	26	49	44	34	83	161
46.5	45	30	22	15	19	25	16	14	40	72
47.0	56	21	24	27	17	21	20	11	33	32
47.5	32	14	18	19	7	21	9	6	5	10
48.0	23	11	11	15	10	16	8	8	4	5
48.5	14	13	7	11	4	22	7	7	1	2
49.0	11	2	6	9	3	10	3	3	1	2
49.5	7	1	4	8	5	3	3	3	4	2
50.0	5	3	1	6	7	7	2	-----	2	1
50.5	1	-----	1	2	2	3	1	-----	-----	-----
51.0	1	3	0	2	2	-----	-----	-----	1	-----
51.5	2	-----	1	-----	-----	1	-----	-----	-----	-----
52.0	-----	-----	2	-----	-----	-----	-----	-----	-----	-----
53.0	-----	-----	-----	2	-----	-----	-----	-----	-----	-----
Total	6,340	8,074	6,817	6,425	5,692	6,211	5,744	4,209	8,194	7,887

In the three series all samples were drawn from purse-seine catches except those for 1926, in which samples from the drift-gill-net fishery were included to augment the very scanty data from late May and early June when most of the purse-seine fleet was off Nova Scotia, and so afforded very few samples from

TABLE 9.—*Length frequencies, in half-centimeter classes, of mackerel in the northern contingent as represented by samples from the spring purse seine fishery along the Nova Scotian coast, area XXI*

Length in centimeters	1926	1927	1928	1929	1930	1931	1932
33.0	------	------	------	------	------	------	------
33.5	------	------	------	------	1	------	------
34.0	------	------	------	------	------	------	------
34.5	------	------	------	------	1	------	------
35.0	------	------	------	------	------	------	------
35.5	------	------	------	------	------	1	------
36.0	1	------	------	1	------	1	------
36.5	1	------	------	------	1	------	------
37.0	5	------	------	------	------	1	------
37.5	6	------	------	------	------	3	4
38.0	24	1	------	------	------	11	3
38.5	52	2	------	------	------	14	9
39.0	105	8	3	------	------	27	18
39.5	199	7	1	------	1	22	40
40.0	259	13	10	1	------	11	57
40.5	271	24	12	6	------	5	45
41.0	239	28	30	15	------	4	40
41.5	115	38	38	28	------	3	26
42.0	76	19	55	55	------	2	9
42.5	44	13	57	79	1	2	5
43.0	29	4	45	109	7	4	23
43.5	22	2	30	97	6	7	26
44.0	32	4	22	127	12	12	41
44.5	40	1	6	94	12	18	53
45.0	48	5	9	62	10	15	74
45.5	44	3	6	33	18	17	62
46.0	58	6	4	16	7	13	60
46.5	54	5	4	23	5	5	32
47.0	44	8	2	22	4	7	28
47.5	29	6	3	15	4	5	10
48.0	16	1	1	12	2	------	15
48.5	14	1	1	7	------	------	10
49.0	9	1	------	6	------	1	4
49.5	8	------	1	2	------	2	5
50.0	6	------	------	5	------	1	3
50.5	5	------	------	5	------	------	2
51.0	2	------	------	1	------	------	------
51.5	1	------	------	1	------	1	------
52.0	1	------	------	------	------	------	1
52.5	1	------	------	------	------	------	------
53.0	------	------	------	------	------	------	------
53.5	------	------	------	------	------	------	------
54.0	------	------	------	------	------	------	------
Total	1,860	200	340	822	92	215	705

the area in which the mixed population occurred.[15] For convenience in referring to the modes in the frequency distributions of figure 10, identifying letters have been inserted at about the modal positions. The modes are composed of either a single year class or of groups of year classes as is obvious from the fact that they progress toward larger sizes through successive years.

For the first 4 years, 1926 to 1929, mode A was consistently present and dominated the northern contingent, progressing from 40.5 centimeters to 43.5 centimeters. Mode B similarly was consistently present and dominated the southern contingent, progressing from 37.8 centimeters in 1926 to 41.5 in 1929. The mixed population appears to have elements of both modes with A definitely represented most strongly in 1926 and 1927. In the next 2 years, when evidently there was more nearly equal representation of the two groups, there is a mode intermediate between A and B.

In 1930, mode A continued dominant in the northern contingent but the shape of the curve is irregular due to chance fluctuations within the small sample of Nova-Scotian-caught fish available in that year. Mode B of the southern contingent probably should be located at 42.0 centimeters but a hump appears at 43.0 centimeters. The latter may be due in part to random sampling fluctuations and in part to the presence of a few samples that might better have been included with the mixed population. A new and strong mode at C appears in the southern contingent.

In 1931, there is a combination of modes which has already been examined in detail in the 1932 material. Mode A continues present in the northern contingent, B in the southern contingent, and C in both contingents. The latter is definitely stronger in the northern contingent where it appears to have strength about equal to that of mode A but relatively weaker in the southern contingent where it seems less than one-fourth as strong as mode B. As above remarked, this relationship continues in 1932, when also mode ED (see also p. 286) makes its appearance in the southern contingent.

Subsequent to 1933 there is less clarity, due to lack of samples from the coast of Nova Scotia, and to the less-well-marked separation of modes. Nonetheless, the before-noted relationships within the A–B–C modal complex persisted through these last 3 years about as might be expected from the previous years. The new mode at E is difficult to interpret for lack of Nova Scotia material to serve as a model by which to judge the northern contingent's length composition.

From 1926 to 1932, however, it is clear that the catches of mackerel from the late spring runs off southern New England are separable into two groups of markedly different length composition. One group, which has been named southern contingent has a size composition which is clearly distinct from that in the run that appears off the coast of Nova Scotia and which has been termed northern contingent. The other group in the catches off southern New England forms frequency distributions such as might be expected if the northern contingent mixed with the southern contingent in these areas. The data for 1933, 1934, and 1935 are

[15] In general, throughout this report, the combining of purse-seine and drift-gill-net data has been avoided inasmuch as the latter gear may be size selective and possibly be misleading. In this particular case, the gill-net samples dominate both the distribution representing the mixed population and the distribution representing the southern contingent, and it is quite obvious that net selection was not sufficient to obscure the difference between the two, although the modes may be slightly displaced in the gill-net material as compared with the purse-seine material.

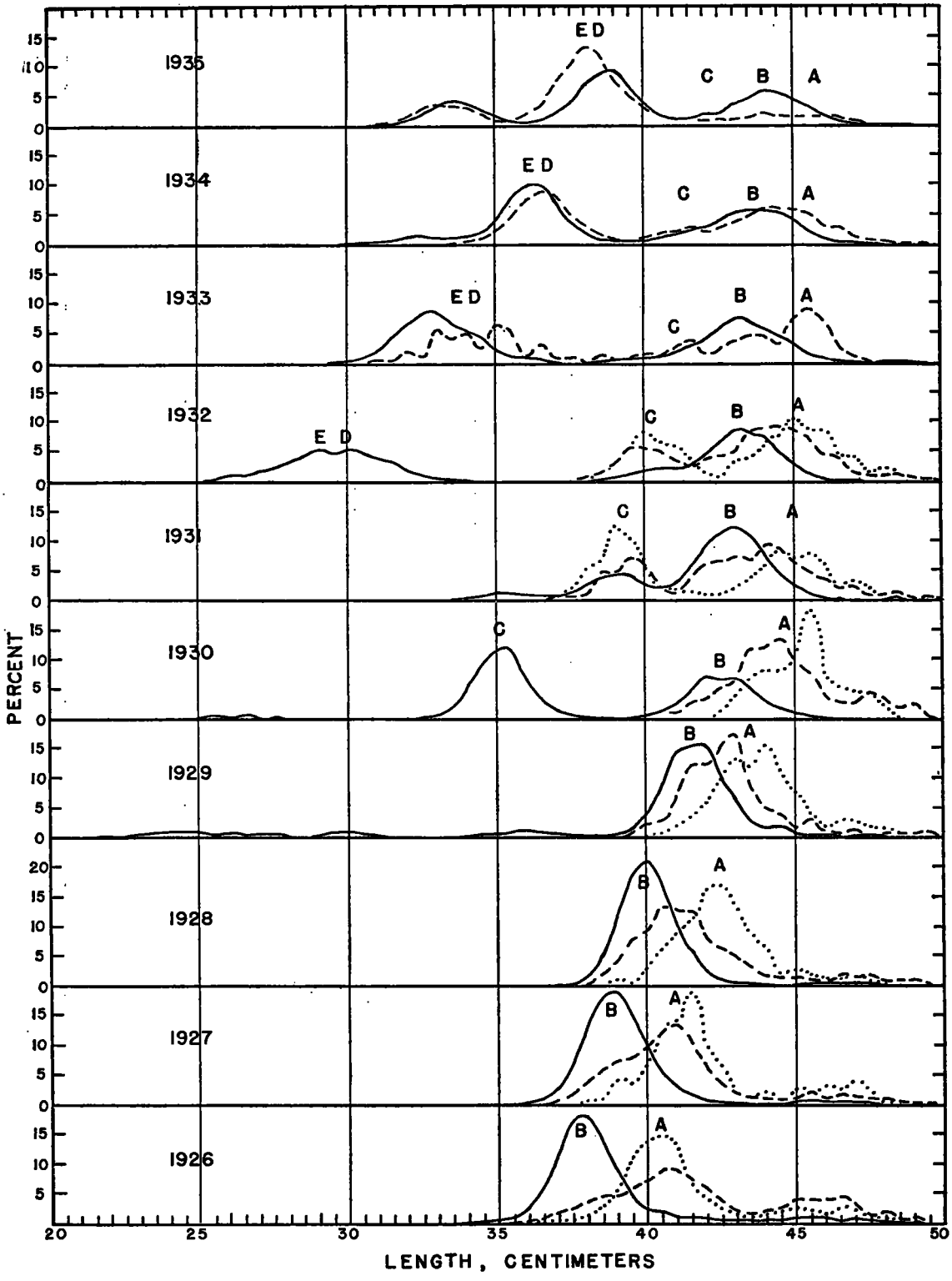


FIGURE 10.—Distribution of lengths of mackerel during May and June for the years 1926 to 1935, in three catagories—those referable to the southern contingent (solid line), northern contingent (dotted line), and to the mixed population (dashed line) comprising elements of both.

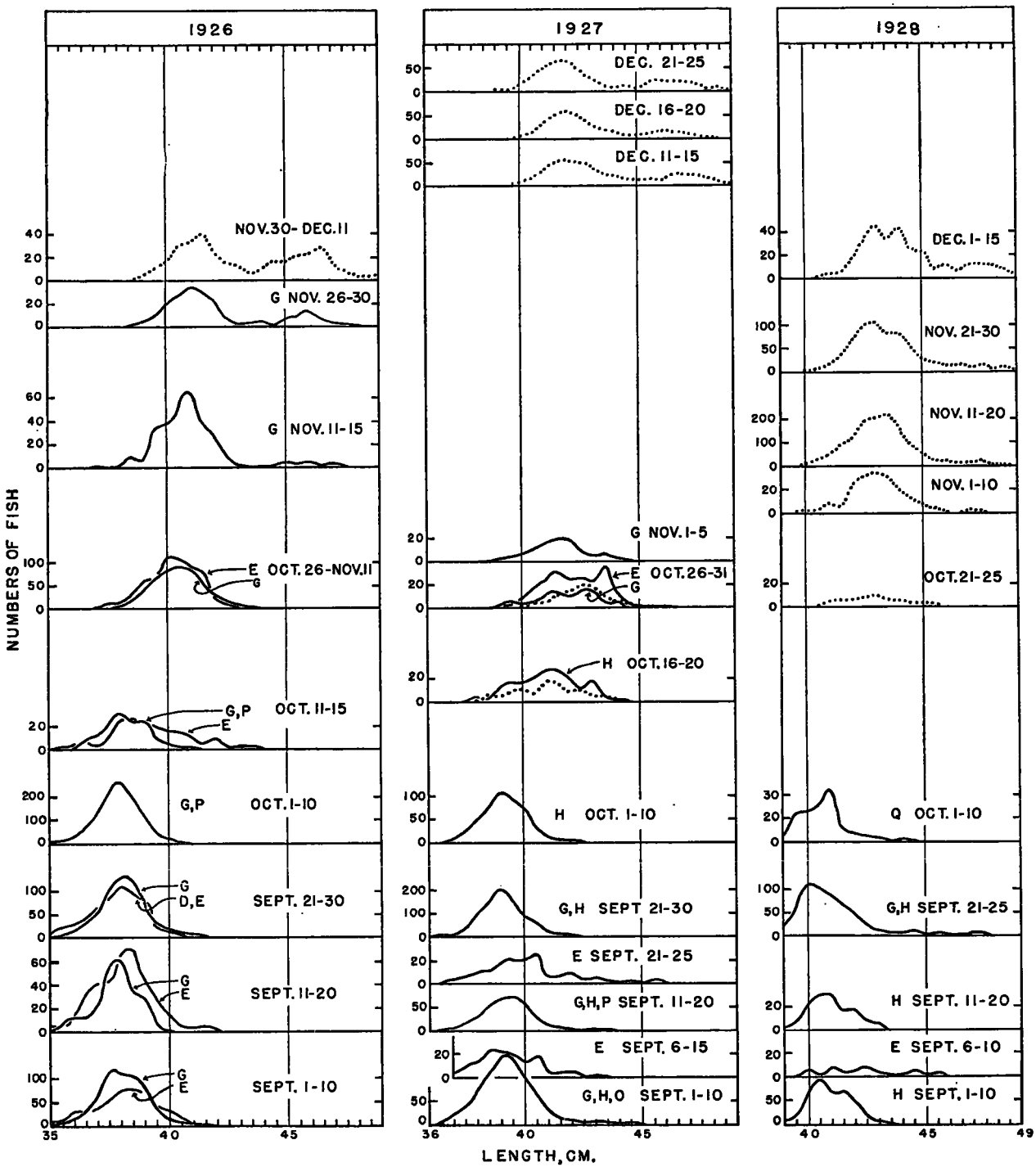


FIGURE 11.—Length composition of medium and large mackerel in catches off New England during the fall months in 1926, 1927, and 1928. Solid lines represent purse-seine catches from the subareas of statistical area XXII designated by letters. Dotted lines represent drift-gill-net catches, all of which were made in subarea E of statistical area XXII. The base lines of the curves are spaced vertically in approximate proportion to calendar date.

less decisive but they are not inconsistent with this conclusion.

In the fall of the year there is a characteristic change in size composition similar to the one that takes place in the spring. This is demonstrated in detail in figure 11 for three autumns—1926, 1927, and 1928. In preparing this figure, working graphs were drawn for the samples from each subarea of statistical area XXII (the only area fished by the American fleet at this season of the year) for each short time interval of 5 days and often less. Space does not admit of reproduction in such detail of these many curves. For this reason the data were grouped in longer time intervals, usually 10 days for figure 11, wherever this could be done without obscuring essential details. However, the source of samples and the aggregate numbers of individual measurements available daily from each area are given in tables 20 and 22 and the frequency data either by weekly or by 10-day periods in tables 21 and 23. The curves of figure 11 were drawn through the unsmoothed frequency values and are irregular where the numbers are few.

When the irregularities associated with small numbers are disregarded, it is evident that in each of the 3 years from the 1st of September to the 10th of October the catches from the various areas through the successive time periods were of essentially uniform size composition.[16] Following October 10 the few samples available from mid-October indicate that the size composition had become unstable. The mode which had been pronounced and relatively constant throughout September and the first 10 days of October at about 38 centimeters in 1926, 39 centimeters in 1927, and 40.5 centimeters in 1928 tended to disappear; and there was a marked accretion of fish several centimeters longer. These tended to form a mode at a point where formerly there was a mere "tail" in the distribution. By the last days of October there were practically no fish left at lengths which had been modal during September and early October. Instead a strong mode appeared at about 41 centimeters in 1926, 42 centimeters in 1927, and 43 centimeters in 1928. In addition to the dominant mode there is a secondary one at 41 to 42 centimeters in most of the curves.

[16] There is a relatively small but consistent difference between the mackerel caught north of Cape Cod (subareas D and E) and those southeast and south of Cape Cod (subareas G, H, O, P, and Q). The significance of this small difference will be discussed in later sections on the summer sojourn and the fall return. For the time being it is sufficient to note that the difference within this segment of time and space is far less than the change that took place after October 10 in all 3 years.

For purposes of discussion the period of stability through September and early October may be called "early fall," the mid-October period of instability may be called the "midfall transition" and the period of stability through November and into December may be called "late fall."

Using these designations it is obvious that the population of early fall has a size composition entirely different from that in the late fall. The difference is too extreme to be attributed to anything other than a change in the population between early and late fall—in other words—the existence of two populations; one succeeding the other in the same region. It is apparent, too, from figure 11, that the midfall transition is a period when elements of both populations are evident in the samples. These appear in the panel for October 11–15 in 1926 and for October 16–20 in 1927.

It is further evident by comparison of the curves of figure 11 with those in the three lower panels of figure 10, that the early fall population had a length composition identifying it with the spring southern contingent while the late fall population may similarly be identified with the northern contingent as it was sampled by the spring catch off Nova Scotia. The midfall transition has its mixed population comparable to the spring mixed population which was studied in some detail, but the sampling was too sparse during the midfall transition to repay intensive examination of the material.

Length-frequency distribution curves for short time intervals during autumn for the remaining 7 years of the investigation prove that the change from one population in early fall to another in late fall occurred consistently, year after year. Space does not permit reproduction of these hundreds of frequency curves, but the length compositions characteristic of the two populations are shown for all 10 years in the "fall" panels of figure 12.

The data for the curves in these fall panels were assembled as follows: Curves were plotted for each date-locality group of samples listed in table 23. September 1 was initially selected as the arbitrary starting point for each fall series but paucity of medium and large mackerel in the September catch and consequently in the samples during September in some years led to the inclusion of a portion of August in such years in order to get a representation of these sizes. From inspection of each season's series it was obvious that termination of the purse-seine fishery and initiation of the drift-gill-net

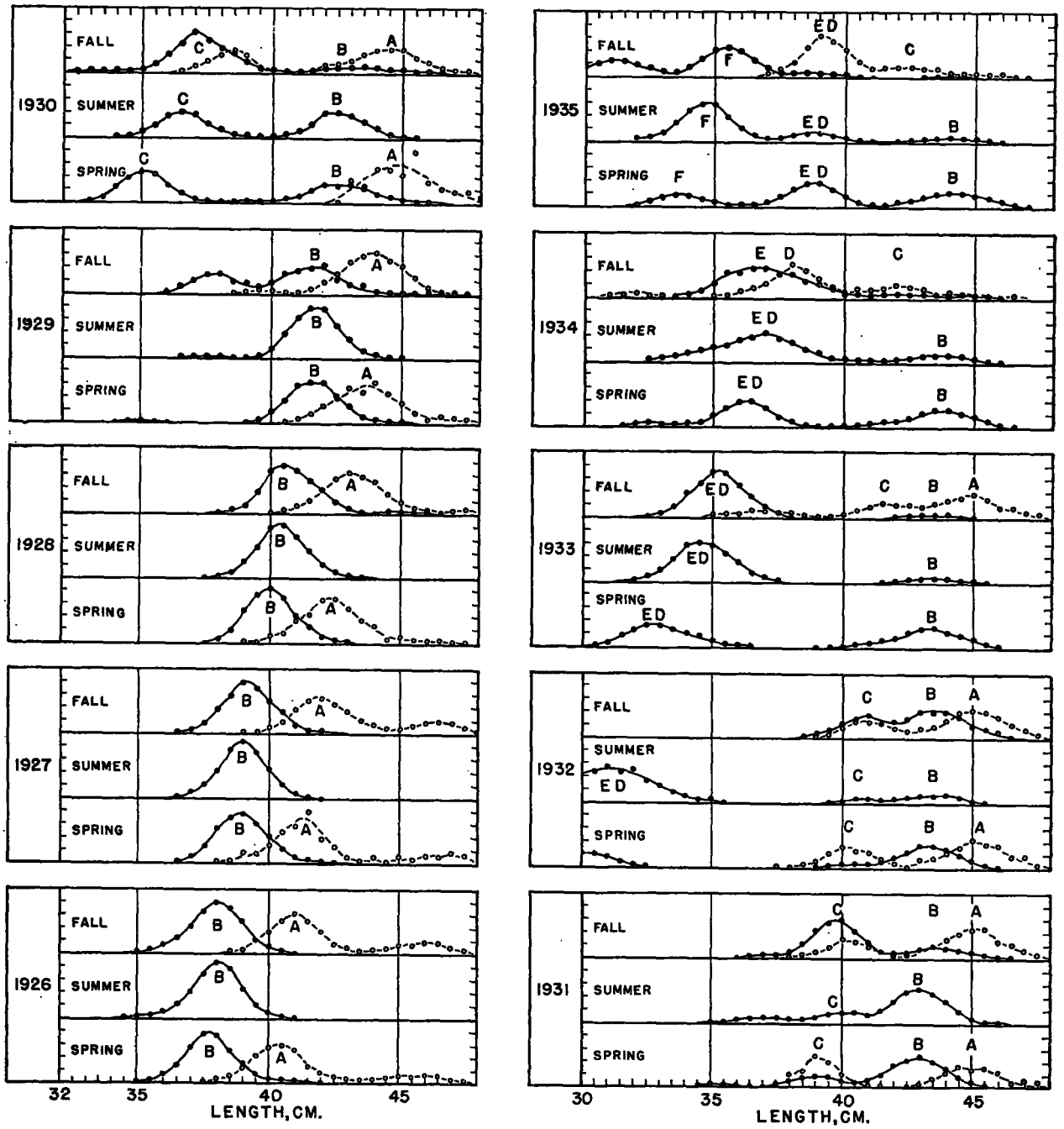


FIGURE 12.—Length-frequency distributions illustrating the size composition of the two types of mackerel population: southern contingent (solid dots and solid lines) and northern contingent (open circles and broken lines), during 10 seasons. The curves are on a percentage basis and the graduation marks on the vertical axis represent 5 percent intervals.

fishery nearly coincided with the "mid-fall transition" in all years except 1926. To avoid heterogeneity with respect to catching method, it was decided to include as early fall category all purse-seine samples up to date-group first showing, by a change in size composition such as registered October 11–15 in 1926 and October 16–20 in 1927 (fig. 11), evidence of a change in population, and to include as late fall category all drift-gill-net samples after the size composition showed stability by essential uniformity

of the curves through successive 5-day (or weekly in some instances) periods. The resulting groups are listed in table 10 and the summed frequencies for early fall in table 11 and for late fall in table 12. These summed frequencies, converted to equal areas by computing the percentage of fish in each size class were plotted in the "fall" panels of figure 12 and smooth curves drawn either through the points or in such relation to the points that the deviations above and below were in balance and the square of each deviation (in actual, not percentage, numbers of fish) of the curve from the point is less than the number of fish in the class. This is intended to fulfill, roughly, the requirement that the smoothed curve "fits" the empirical data, with a confidence above the P=0.05 level as judged by the chi-square test. Actually no rigorous test is possible for want of definitive knowledge as to the number of degrees of freedom absorbed in such "free-hand" curve fitting.

TABLE 10.—*Organization of data in tables 11 and 12*

Item	Included as "early fall" in table 11		Excluded from tables 11 and 12		Included as "late fall" in table 12	
	Period	Number of fish	Period	Number of fish	Period	Number of fish
1926:						
Purse seine	Sept. 1–Oct. 10	4,060	Oct. 11–Nov. 10	1,420		
Drift gill net					Nov. 11–Dec. 11	873
1927:						
Purse seine	Sept. 1–Oct. 10	3,030	Oct. 11–Nov. 10	580		
Drift gill net			Oct. 11–31	200	Dec. 11–25	1,260
1928:						
Purse seine	Sept. 1–Oct. 10	1,415				
Drift gill net					Oct. 21–Dec. 5	2,540
1929:						
Purse seine	Aug. 21–Sept. 20	1,044	Sept. 21–Oct. 10	55		
Drift gill net			Sept. 21–25	60	Oct. 21–Nov. 15	1,430
1930:						
Purse seine	Aug. 11–Oct. 25	3,015				
Drift gill net			Sept. 21–Oct. 20	70	Oct. 21–Dec. 5	2,453
1931:						
Purse seine	Aug. 11–Oct. 31	3,912				
Drift gill net			Oct. 21–Nov. 10	270	Nov. 11–Dec. 7	1,865
1932:						
Purse seine	Aug. 11–Oct. 5	1,751				
Drift gill net					Sept. 26–Dec. 15	2,535
1933:						
Purse seine	Aug. 27–Sept. 30	3,701	Oct. 1–Nov. 4	3,077		
Drift gill net					Oct. 29–Dec. 14	3,197
1934:						
Purse seine	Sept. 21–Oct. 20	2,338				
Drift gill net					Nov. 13–Dec. 5	1,209
1935:						
Purse seine	Sept. 1–Nov. 11	115				
Drift gill net					Nov. 1–Dec. 20	3,602

TABLE 11.—*Length composition of mackerel in the "early fall" period, 1926 to 1935*

Length in centimeters	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	Total
23.0										1	1
25.0										1	1
26.0										1	1
27.0										1	1
27.5										6	6
28.0										16	16
28.5										55	55
29.0									1	115	116
29.5										225	225
30.0					1					397	398
30.5					6					549	555
31.0	1				2				2	673	678
31.5	1				5					632	638
32.0	4	2			8			2	4	518	538
32.5	7	2		1	15	1		8	7	344	385
33.0	13	8		5	20	2	1	36	9	243	337
33.5	11	1		2	18	1		103	12	197	345
34.0	10	2		6	30	2		229	22	378	679
34.5	11	1		4	25	3		389	64	719	1,216
35.0	28	2		6	43	6	3	597	119	1,121	1,925
35.5	66	3		1	107	10	2	615	231	1,262	2,297
36.0	130	4		10	221	13	1	447	217	1,099	2,142
36.5	243	20		30	345	37	3	350	257	748	2,032
37.0	416	53	2	50	468	55	2	175	261	397	1,877
37.5	672	130		74	388	51	2	68	206	175	1,762
38.0	799	295	6	75	274	110	5	26	216	175	1,977
38.5	700	437	15	50	215	208	14	21	145	169	1,962

TABLE 11.—*Length composition of mackerel in the "early fall" period, 1926 to 1935*—Continued

Length in centimeters	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	Total
39.0	502	599	41	43	124	419	36	7	129	217	2,093
39.5	203	536	115	30	49	518	55	8	74	141	1,691
40.0	144	389	236	45	35	558	94	11	39	95	1,581
40.5	44	257	254	81	18	400	134	11	33	57	1,266
41.0	15	96	235	92	29	226	152	34	19	33	916
41.5	17	55	174	103	39	119	107	40	37	22	704
42.0	9	39	130	113	53	111	110	65	29	23	675
42.5	4	13	66	58	57	123	129	75	30	33	576
43.0	2	20	37	39	58	148	177	85	32	44	633
43.5	2	12	11	36	77	174	170	75	33	44	625
44.0	2	11	9	12	63	166	185	81	22	53	591
44.5	3	8	17	12	50	124	141	60	30	41	478
45.0	4	8	11	6	46	115	87	45	26	31	372
45.5	4	5	10	8	21	74	63	17	17	32	247
46.0	4	5	8	8	31	61	41	11	9	15	185
46.5	2	3	5	9	17	29	14	2	2	13	94
47.0	1	5	9	8	16	17	10	2	2	2	70
47.5	3	3	7	6	11	12	7	4			52
48.0	4	3	4	4	13	8	3				39
48.5	5	1	4	8	7	2	2	2	2		33
49.0	1	1	4	5	4	6				1	21
49.5	2	1	2	2	1		1				9
50.0	1		2		2						5
50.5					1	1					2
51.0				1	1	1					3
51.5					1						1
52.0				1		1				1	3
54.0			1								1
Total	4,060	3,030	1,415	1,044	3,015	3,912	1,751	3,701	2,338	11,115	35,131

TABLE 12.—*Length composition of mackerel in the "late fall" period, 1926 to 1936*

Length in centimeters	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	Total
28.5										1	1
29.5									1		1
30.0				1							1
30.5						1			4		5
31.0									8		8
31.5									12		12
32.0									22		22
32.5									6		6
33.0									9		9
33.5								1	3		4
34.0					1		1	14	5		21
34.5					1		1	11	4		17
35.0					2		5	37	10		54
35.5					1		3	54	14	2	74
36.0				1	4		1	54	32	3	95
36.5				1	14		2	82	46	9	154
37.0	1				59	2	3	86	67	52	270
37.5	1	1		1	107	5	1	76	104	108	404
38.0	2			5	167	12	4	63	152	199	604
38.5	10			6	208	26	4	40	125	414	833
39.0	14	7		10	165	49	16	33	90	569	953
39.5	51	5	3	20	71	77	41	31	52	506	857
40.0	72	27	11	15	42	141	101	62	32	395	898
40.5	109	58	34	10	26	117	167	105	40	222	888
41.0	132	116	76	13	25	86	152	140	36	123	899
41.5	109	161	133	28	25	46	136	184	47	141	1,010
42.0	78	174	226	67	80	27	102	166	57	130	1,107
42.5	34	145	350	110	86	30	75	159	50	146	1,185
43.0	21	106	394	174	111	55	94	143	39	118	1,255
43.5	12	64	364	213	173	84	110	181	24	113	1,338
44.0	15	47	315	224	212	135	177	220	27	72	1,444
44.5	20	34	198	185	225	178	255	250	18	61	1,424
45.0	28	26	123	154	228	215	265	291	24	63	1,417
45.5	32	43	60	91	145	216	253	227	17	45	1,129
46.0	40	52	50	37	101	129	202	145	12	54	822
46.5	38	59	38	26	56	103	143	136	10	23	632
47.0	22	57	39	14	41	54	80	84	3	17	411
47.5	13	30	51	14	28	36	47	50	4	12	285
48.0	6	16	25	7	17	17	34	21	1	2	146
48.5	5	12	23		9	9	21	17		1	97
49.0	4	5	14	2	7	7	16	15	1	1	72
49.5	1	5	6		3	2	13	13	1		44
50.0	2	2	2		4	5	4	3			22
50.5		5			2	1	3	2			13
51.0	1	2	4		2		1	1			11
51.5			1		3		2				6
52.0		1		1	1						3
52.5					1						1
Total	873	1,260	2,540	1,430	2,453	1,865	2,535	3,197	1,209	3,602	20,964

The resulting sets of curves shown in the panels labeled "Fall," in which the curves of the early fall category have been drawn with solid lines and those of the late fall with broken lines, demonstrate that there was a marked difference between the early and the late fall populations every year. The difference was comparable in degree and in character to the differences previously noted in spring. That is, the fall fishery gives evidence of regularly drawing on two different contingents of mackerel, just as was found true of the spring fishery.

NATURE OF THE TWO CONTINGENTS

In applying a name to the two recognizably different parts of the mackerel population the term "contingent" was selected in order to avoid terms such as "race," "subspecies," or "variety," which have acquired particular technical connotation through their use in fisheries and in micro-systematics. The search for a technically noncommittal term has resulted in the choice of a word that is appropriate only in the sense of one of its less common meanings, that is, "any of the local groups of an assemblage" (Webster's New International Dictionary of the English Language, second edition, unabridged, G. & C. Merriam Co., 1944). As used here, the adjective "local" should be omitted from the definition, since it is not desired for the time being, at least, to imply any specific local geographical affinity.

Having adopted a noncommittal term, it is possible, without prejudice, to discuss the nature of the two groups within the mackerel population which are here designated as southern contingent and northern contingent.

For purposes of this discussion the principal reference will be to figure 12. The composition of the frequency distributions described by the curves in the panels labeled "fall" has already been given. The curves in the panels labeled "spring" are the same ones as given in figure 10 omitting the so-called mixed population and smoothing as described for the curves of the fall panels. The curves of the panels labeled "summer" simply are summed frequencies of all mackerel catches sampled between the end of the spring period and the beginning of the fall period (i. e., June 30 of each year, to the particular date listed in table 10 for the beginning of the "early fall" period) converted to percentage and smoothed as described for the curves in the fall panels. Although this assemblage of curves involves omission of some blocks of data [17] it contains all of the characteristic length-frequency groupings found in the catches of the United States vessel fishery for mackerel during the 10-year period except the "mixed" populations of spring and fall as these were defined in the preceding section. The curves on the intermediate size compositions during these periods of mixing are essential to this discussion but could not be included in figure 12 without either making a confusing tangle of lines or multiplying the panels beyond graphic utility.

Reviewing, now, the times and localities represented by the various blocks of data: the catch off the United States coast south of Cape Cod in the springtime was composed purely of the southern contingent except for a brief period in late May and early June (figs. 7 and 8) when members of the northern contingent mixed with them (broken-line curves in fig. 10). In late May and early June also, in years when American mackerel vessels fished along the coast of Nova Scotia they caught only the northern contingent there (broken-line curves in the spring panels of fig. 12). After the brief period of mixing along the United States coast in late May and early June, the catch reverted to southern contingent mackerel and continued to be comprised of such mackerel through summer and early fall. At the latter time or shortly thereafter the southern contingent disappeared and with its disappearance the purse-seine fishery usually terminated. However, at this time northern contingent mackerel appeared in the Gulf of Maine and continued to furnish catches to the drift-gill-netters through late fall and sometimes well into December, before they disappeared and the mackerel fishing season ended.

From this succession of events, practically the only possible conclusion is that the southern contingent is a body of mackerel that appears in early spring well south of Cape Cod, proceeds northerly along the coast and into the Gulf of Maine to spend the summer, and then disappears again in midfall; whereas, the northern contingent appears in late spring briefly off southern New England, moves quickly to the coast of Nova Scotia, and passes out of the range of the modern American fishery, returning again in late fall through the Gulf of Maine as it moves to its winter grounds. Thus, the two contingents are bodies of mackerel of different size

[17] Omitted are (1) all small or yearling mackerel (because not here under consideration), (2) samples prior to May 1 and all drift-gill-net fishery samples of the spring period (these do not differ from the solid line curves in the spring panels of fig. 12 in any way that is material to the present discussion).

composition and different migrating habits. The southern contingent appears earlier in the spring, spends the summer in more southerly waters, and disappears earlier in the fall than the northern contingent. But a large part of the routes of both contingents is through the same waters, and at particular times of the year they are in the same waters together.

Recalling that the two principal spawning grounds of the American mackerel are widely separated, a southern one being in the great oceanic bight between Cape Cod and Cape Hatteras and a northern one in the Gulf of St. Lawrence (Sette 1943), and noting that the southern contingent is on the southern spawning ground in spawning season and the northern contingent, when last evident to our fishery, is well beyond this on a route leading to the Gulf of St. Lawrence prior to the time spawning takes place there, it would appear that the two contingents are well separated from each other when spawning. This separation during reproduction would favor an hypothesis that the two contingents were generically distinct races. Eventually this may prove to be true. For the present, however, it does not appear to be consistent with other evidence, some of which is contained in figure 12.

The most striking features of figure 12 are the prominent modes and their progression to successively greater fish lengths through successive years. Both of these features are so prominent and so consistent that there is no difficulty in identifying homologous modes. Several series of them have been marked with the letters A, B, C, etc. It is obvious that each mode is comprised of a single year class or a group of year classes and the progression of homologous modes is due to growth of the members of the particular year classes. Anticipating the results of a partially completed study of age, it is provisionally determined that mode A is comprised mainly of the 1921 class, mode B of the 1923 class, mode C of the 1928 class and mode D of the 1930 class. The latter apparently was a class of atypically slow growth during early life and was soon overtaken by the 1931 class, so that both the 1930 and 1931 classes contribute to the mode labeled ED from 1932 to the end of the series. Mode F is the 1932 class.

According to this interpretation, a number of year classes were missing or present in very small numbers. It is to the absence of year classes that the wide separation of the modes may be attributed. More important, it is the absence of different year classes in the two contingents, particularly during the first 7 years of the series, that underlies the characteristic difference of the contingents in size composition and permits them to be distinguished one from the other. The consistent absence of mode A in the southern contingent and of mode B in the northern contingent is a prime example of this.

On the other hand, some modes are not as consistently absent from one contingent or the other. Mode C, for instance, was present in both contingents. In 1930 when it first appeared this mode was most strongly represented in the southern contingent. In later years it tended to decline in the southern contingent and increase in the northern contingent. By 1933 and 1934 it had declined in the southern contingent so severely that it was barely perceptible while it still was prominent in the northern contingent. This suggests that members of a year class may transfer from one contingent to another. If this does happen, the genetic strains of the two contingents could not remain distinct.

However, the evidence that members of a year class transfer from one contingent to the other is far from conclusive. The curves of figure 12 are on a percentage basis and a given mode may be prominent or not, depending on the numbers of fish in the remaining portions of the distribution. Thus C declines in the southern contingent when ED joins the stock and fails to decline correspondingly in the northern contingent because new recruits such as ED did not join that contingent in proportionately as large numbers. However, the changes in C relative to B in the southern contingent and C relative to A in the northern contingent are not subject to this effect and could be changed only by a differential mortality, by an emigration out of or by immigration into the stock. The questions then become: (1) In the southern contingent did C decline relative to B due to a higher mortality than B or due to emigration from the stock? (2) In the northern contingent did C increase relative to A in the northern contingent due to a higher rate of mortality in A than in C or due to immigration of C into the stock of the northern contingent?

The first alternative in each instance would not be contradictory to the hypothesis of genetic separation of the two contingents while the second alternative would be. At present, knowledge is not sufficient to definitely select one alternative or the other.

There is the further question: Was the sampling

of the two stocks sufficiently representative to warrant the drawing of conclusions from the proportionate heights of the several modes? While I have considerable confidence that the sampling of the catch was not seriously biased in favor of one group of sizes as opposed to another, a similar confidence cannot be placed in the nonselective nature of the fishermen's catch from the existing stock. Indeed, there is abundant indication, especially marked in some seasons, that the several size groups are selectively "available" to the fishery. One particularly marked phase of this will be discussed in a later section.

It is possible that some light may be thrown on this and the two preceding questions by further analyses involving abundance indices. Preliminary work of this nature has suggested that some year classes, as sampled by the commercial fishery, have disappeared from the stock drawn upon by the United States fleet at a moderate rate of about 20 percent per annum and others at a much higher rate in the neighborhood of 80 percent per annum during successive years in the fishery (Sette 1933, 1934). The ones disappearing at a slow rate were termed "persistent" year classes; the ones disappearing at a high rate "transitory" year classes. The rate of disappearance may be due either to mortality or to departure of members of the year class from the stock fished by the United States fleet, or a combination of the two. Since the southern contingent is the principal stock fished by the United States fleet, the departure of members from year classes in this contingent to join the northern contingent would produce the effect noted for the transitory year classes. Those year classes not departing from the southern contingent would diminish only from mortality and so would have some lesser rate of disappearance. Among the year classes classified as persistent or transitory (classes 1923 to 1929, inclusive), and also abundant enough to create prominent modes (classes 1923 and 1928), the 1923 class formed mode B which was consistently present in the southern contingent and consistently absent in the northern contingent, and the 1928 class formed mode C which was relatively more prominent in the southern contingent early in mature life and later became relatively more prominent in the northern contingent. Thus, provisionally at least, the weight of evidence, if not definitely in favor of the shift of individuals from one contingent to the other, at least is sufficiently suggestive of this to prevent adoption of the view that the two contingents maintain their integrity throughout life and from one generation to another, as would be necessary for postulation of genetically separate stocks.

An even simpler view as to the phenomenon underlying the existence of the two contingents, is that mackerel have a southerly distribution when young and comprise the southern contingent and that the mackerel extend their migration farther north as they enter the later years of life and comprise the northern contingent. This would be consistent with the evidence afforded by the 1928 class of mode C but would be utterly contrary to the behavior of the 1923 class of mode B which continued prominent in the southern contingent for more than 9 years and never was represented strongly enough in the northern contingent to be detectable.

Thus it does not seem possible, at present, to define the biological nature of the contingents more explicitly than to say that they are aggregates of mackerel migrating as units that are recognizable by the configurations of their length-frequency curves, and the configurations are sufficiently stable from spring to fall and from one season to another to suggest that the majority of the individuals retain their memberships in the same contingent through a number of years though not necessarily throughout life, nor from one generation to another.

In conclusion, it appears that the adult stock of mackerel contains two populations which migrate along the coast in the springtime, each composed of a different complex of year classes which causes the distinctive size composition by which they are recognized. The one most southerly in the place of its first appearance (off the Virginia Capes) and its final destination (the Gulf of Maine) is termed the southern contingent, while the one more northerly in the place of its first appearance (off southern New England) and in its final destination (Nova Scotia and the Gulf of St. Lawrence) is termed the northern contingent. During a portion of the migration (past southern New England) these contingents are mixed in demonstrable proportions. The southern contingent spends the summer and early fall in waters off New England and disappears in late fall. At about this time the northern contingent populates these waters, presumably on its way from Canadian waters to its winter quarters. Various aspects of the migrations of each contingent remain to be considered in detail. As yet, there is

no positive evidence as to whether the two contingents inhabit the same waters in the wintertime and are then mixed, separating when their respective spring migrations are performed, or whether the southern contingent winters mainly in the southerly portion of the warm zone at the edge of the continental shelf, say abreast of Long Island and southward, and the northern contingent winters along the edge from abreast of Long Island and eastward. The respective localities of their first appearance render the latter supposition the more likely.

SPRING MIGRATION OF THE SOUTHERN CONTINGENT

First Appearance

The opening of the mackerel season has from early times held such interest that records of first catches were often published. Many of these were assembled by Sette and Needler (1934: 38–39), four by Goode, Collins, Earle, and Clark (1884: 9) and 10 more during the present investigations. From the date of earliest catch in each of the 56 seasons for which this datum is available (fig. 13) it may be calculated statistically that the average date for the opening of the season is April 11, that usually (two out of three times) it opens between April 3 and 19. Since mackerel often may be present some days before the first catch, the date of appearance of the mackerel (as distinguished from the date of catching) must be somewhat earlier and probably is somewhat less variable.

From the 29 available records on the locations of first catches listed in table 13 and plotted in figure 14, it is obvious that the first mackerel of the season are most frequently taken along the outer third of the continental shelf between the thirty-seventh and thirty-eighth parallels of latitude, though they occasionally are found as far south as latitude 35°20′ (near Cape Hatteras) or as far north as latitude 39°0′ (80 miles off Atlantic City) a spread of 200 miles parallel and 60 miles vertical to the coast line. When taken north of latitude 37° (mouth of Chesapeake Bay), they are inclined to be at the outer edge of the shelf, and when south of latitude 37° they may be either inshore or offshore.[18]

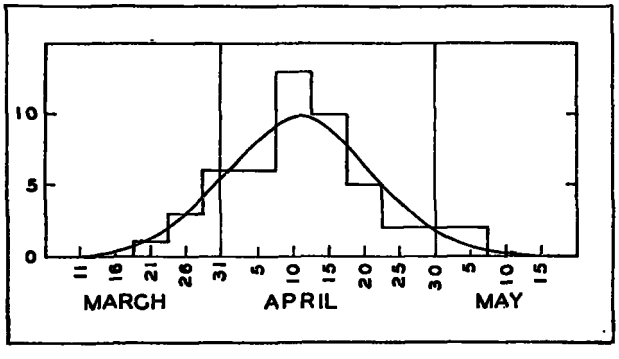


Figure 13.—Date of first catch of the season in various years during the period 1878 to 1935. The histogram represents the number of times the first catch fell in each 5-day period, and the smooth curve describes the corresponding normal probability.

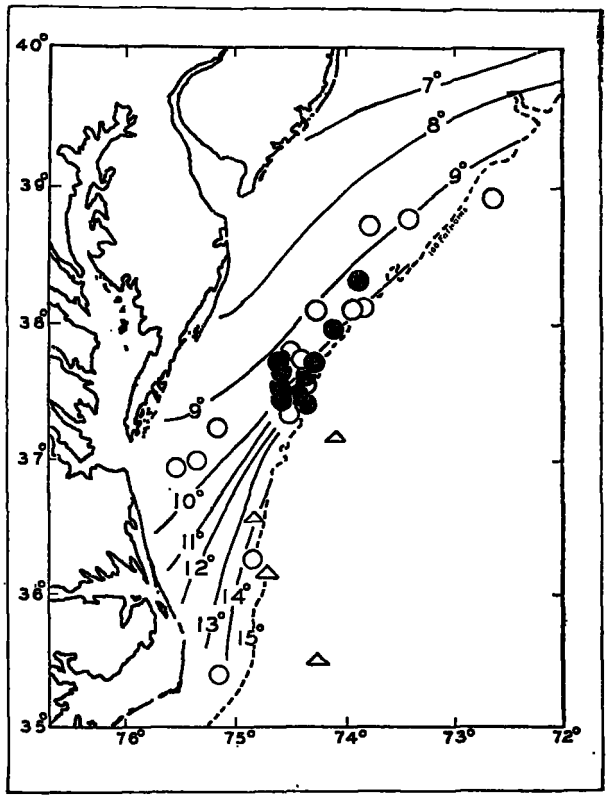


Figure 14.—Position of first catches in each of 29 seasons. Triangles represent seasons 1878 to 1881; open circles, various seasons, 1887 to 1925; solid-black circles, seasons 1926 to 1935. The isotherms relate to the period April 3 to 11, 1930, and illustrate the distribution of surface temperatures at this season.

[18] Although 3 of the 29 positions are well outside the continental shelf area, we are not inclined to place much emphasis on these offshore records because mackerel fishermen for the most part determine their position by "dead-reckoning" and on the long course runs in this southern fishery, a slight lack of precision in designating a bearing or estimating the speed of sailing might easily put the supposed position a number of miles from its true one; and as none of these catch records were particularly noted as being beyond soundings it may be doubted that they were as far offshore as indicated.

TABLE 13.—*Date and locality of "first catch of the season" of mackerel*[1]

Year	Date	Locality
1878	Apr. 16	Lat. 36°10′ N., long. 74°45′ W.
1879	Apr. 12	Lat. 36°35′ N., long. 74°50′ W.
1880	Apr. 1	Lat. 35°30′ N., long. 74°15′ W.
1881	Mar. 20	Lat. 37°10′ N., long. 74°05′ W.
1887	Apr. 21	Lat. 37°20′ N., long. 70°30′ W.
1895	Apr. 17	Lat. 36°20′ N., long. 74°50′ W.
1902	Apr. 9	100 miles south of Barnegat Light.
1903	Apr. 13	85 miles southeast of Barnegat Light.
1904	Apr. 7	30 miles east of Cape Henry.
1905	Apr. 10	40 miles off Cape Henry.
1911	May 1	70 miles southeast of Cape Henlopen.
1914	Apr. 22	50 miles east by north of Cape Charles.
1915	Apr. 9	100 miles east by south of Cape Henlopen.
1916	Apr. 5	80 miles east by south of Cape Henlopen.
1920	Apr. 14	35 miles southeast of Winterquarter Light.
1921	Apr. 7	Lat. 37°50′ N. in 32 fathoms.
1923	Apr. 9	Lat. 37°50′ N. in 30 to 40 fathoms.
1925	Apr. 13	35 miles southeast of Fenwick Island.
1926	Apr. 10	Lat. 37°35′ N., long. 74°35′ W.
1927	Apr. 18	70 miles south ½ east of Cape May.
1928	Apr. 9	25 miles southeast of Winterquarter Lightship.
1929	Apr. 8	75 miles south by east of Cape May.
1930	Apr. 5	80 miles south of Five Fathom Bank Lightship.
1931	Apr. 9	43 miles south of Fenwick Lightship.
1932	Apr. 15	49 miles south of Fenwick Lightship.
1933	Apr. 10	70 miles south-southeast of Cape May.
1934	Apr. 14	90 miles south of Cape May.
1935	Apr. 5	60 miles southeast of Cape May.

[1] Records of 1878 to 1881 from Goode, Collins, Earle, and Clark 1883, p. 9; records of 1887 to 1925 from Sette and Needler, pp. 38–39; records of 1926 to 1935 from present investigations.

VERNAL ADVANCE

After mackerel of the southern contingent first appear in coastal waters they are caught progressively farther north as indicated by figure 7. As earlier mentioned, this has been considered by some as a migration *en masse* of the whole population, by others as separate bodies of mackerel successively approaching coastal waters from directly offshore. My own observations lead to the belief that it is a mass migration but that the main body, as it moves northeasterly parallel to the coast is joined by lesser bodies of fish from farther offshore.

That it is a mass migration is supported by the almost complete disappearance of the mackerel from the region south of Long Island after the brief but productive fishing period in April and May, and by the relatively constant size composition of the population each spring as the fishery advances from the offing of Virginia to southern New England.

That additional schools join the main body as it advances along the coast is indicated (1) by occasional slight changes in size composition of the population, and (2) by the more frequent instances in which bodies of mackerel of slightly different size composition are taken well in advance of the main fishing area, as if the new school had come inshore at a point ahead of the main body.[19]

The passage up the coast is fairly rapid, the center of fishing shifting from the Virginia coast to the Massachusetts coast, a distance of 300 miles, in about 6 weeks. Reaching the neighborhood of southern New England in the midle of May, the southern contingent tarries for nearly 6 weeks; and it is not until nearly the first of July that it usually deserts this ground. In doing so the main body appears to go by way of the southern edge of Nantucket Shoals and through South Channel, judging from the daily shift of the fleets' catches. This does not preclude the possibility of considerable numbers going through Vineyard and Nantucket Sounds or passing right over the Shoals. That some take the route through the Sounds is indicated by catches in pound nets along their shores; that the main body does not do so is evident from the small quantities so caught.

Having passed Nantucket Shoals and arrived in the Gulf of Maine, the southern contingent has reached the grounds of its summer sojourn.

SPRING MIGRATION OF THE NORTHERN CONTINGENT

FIRST APPEARANCE

As previously noted, the mackerel that cause the abrupt alteration in the size composition of the population in southern New England each May are members of the northern contingent; and the alteration is evidence of their first appearance each spring. In Nova Scotia their first appearance is evident simply from the date of the first catch of mackerel. These dates appear in table 14. They refer mostly to the vicinity of Yarmouth. For the 6 years included in the table, the first appearance has been between May 12 and 28 in southern New England

[19] A further argument, based on spawning maturity, is that a "run" of mackerel reaching a given locality often consists of individuals about ready to spawn. Hence the new runs come from offshore rather than from along shore over grounds where mackerel had already spawned. This argument probably is baseless. Moore (1899: 5) found several size classes of eggs in the ovaries of spring-caught mackerel. The existence of such size groups in mackerel ovaries was verified by F. E. Firth (unpublished notes) in the present study. Although Moore's interpretation was that each size group was a season's batch of eggs, it now seems more likely that the groups are due to be spawned at intervals during the season, as was found for the pilchard, *Sardinops caerulea*, (Clark 1934), for the jacksmelt *Atherinopsis californiensis* (Clark 1929), and for the grunion, *Leuresthes tenuis*, (Clark 1925). If this holds true also for the mackerel, appearance of near-ripe individuals in the catch is neither proof that they did not spawn previously nor indication that they came directly from offshore.

and between May 21 and June 4 in Nova Scotia. But the dates of appearance in southern New England of necessity refer not to the very first arrivals of members of the northern contingent, for a few such mackerel would not be detected among the larger numbers of individuals of the southern contingent already there. They refer rather to the arrival in southern New England waters of large numbers of the northern contingent, and for comparability the earliest date of catching large quantities in Nova Scotia must be used. These dates lie between May 24 and June 7 and the lag behind the southern New England appearance is from 0 to 22 days, averaging 12 days over the period in question.

TABLE 14.—*Dates of arrival and departure of the "northern contingent" off southern New England,*[1] *and dates of arrival off Nova Scotia*[2]

Year	Off southern New England		Off Nova Scotia		Number of days between arrival off Southern New England and first catches of large quantities off Nova Scotia
	Arrival	Departure	First catch	First catches of large quantities	
1926	May 28	June 15	May 25	May 28	0
1927	May 16	June 9	do	June 5	20
1928	do	June 6	June 4	June 7	22
1929	May 24	June 7	May 28	June 3	11
1930	May 12	June 2	May 24	May 24	12
1931	May 17	June 6	May 21	May 26	9

[1] As indicated by alteration of the size composition in purse seine catches.
[2] As reported by the Gloucester, Mass., *Times* and the Boston Fish Bureau.

The locality where the northern contingent appears has varied from year to year. During the period in question in southern New England, it has usually been along a rather broad front from as far west as the offing of the eastern end of Long Island (long. 72° W.) to as far east as the vicinity of the Nantucket Shoals Lightship (long. 69°40′ W.), a range alongshore of over 100 miles. Sometimes the first catches of mackerel have been made far inshore. In 1927, for instance, they were first taken close to Block Island. Whether or not this indicates the mackerel of this contingent usually keep to deep levels until close in to land before rising to the surface is not evident from our available information, because fishermen, as a rule, have not explored the offshore waters in this sector, their attention usually being occupied by the southern contingent up to the time the northern contingent appears.

The locality where the northern contingent first appears in Canadian waters in recent years has usually been at the southwesterly end of Nova Scotia.[20] During the 7 years 1926 to 1932, United States purse-seiners fishing off Nova Scotia have located their first mackerel at various points along the coast from off Yarmouth to Scatari Island, but on no occasion were these catches made on dates earlier than mackerel reported (by the press or by trade bulletins) at Yarmouth. Until additional data are available on this subject it would seem that mackerel strike in along a considerable extent of the Nova Scotia coast almost simultaneously but with a general tendency to arrive earliest at the southwesterly end.

VERNAL ADVANCE

Since the northern contingent appears in two widely separated regions, southern New England and Nova Scotia, the advance from each place will be considered in turn.

Off southern New England the northern contingent, having appeared along the coast from Long Island to Nantucket Shoals, rapidly moves eastward, usually reaching the southern border of Nantucket Shoals in about 2 weeks. From here the major portion goes to the coast of Nova Scotia and a minor portion enters the Gulf of Maine. The course taken is somewhat in doubt, but it is probable that the mass movement is directly across the outer portion of the Gulf of Maine (Georges Bank), with a small fraction rounding Cape Cod into Massachusetts Bay, and still others circling back from the southwestern tip of Nova Scotia, thence, along the coast of Maine and even down to Massachusetts Bay. Pound nets, traps, and weirs, located along the shores of that Bay, according to daily catch records during four recent years, usually take their first mackerel earliest at Gloucester, next at Provincetown, and last at Sandwich and Barnstable, strongly suggesting a north to south movement such as would result from the fish circling back. On the other hand, the usual absence of catches along the coast of Maine this early in the season casts doubt upon it.

Whatever course may be taken by those of the northern contingent that enter the inner parts of the Gulf of Maine, it is evident from the small catches here,[21] that only a small fraction of the northern

[20] Huntsman (1922), on the contrary, reported earlier appearance at Cape Breton (May 5) than at Yarmouth (May 16) in 1894.

[21] Later, when the southern contingent enters the Bay, the catches become large. That these larger catches are of the southern rather than the northern contingent is obvious from the sizes of the individuals caught.

contingent is involved and that the major portion goes to the coast of Nova Scotia where it supports an important Canadian shore fishery and where, in many seasons, American purse seiners make large catches offshore.

Information on the advance of the major portion of the northern contingent along the Canadian coast is somewhat meager. During the 10 years of this investigation, only in 1926 did the purse-seine fleet fish along the Nova Scotian coast over a long enough period to cast some light on this question. From table 15 it is evident that the fishery took place off the central portion in the first few days of June, off the eastern portion between the 5th and 10th and in the Canso region between the 11th and 15th of June. Although the fishery progressed along the coast, it cannot be assumed that the fish did.

TABLE 15.—*Progress of mackerel along the Nova Scotian coast in 1926 as indicated by the number of catches made by United States mackerel purse-seiners in each area each day*

Date	Area XXII O (southern Nova Scotia)	Area XXII M (central Nova Scotia)	Area XXII K (eastern Nova Scotia)	Area XXII D (Canso)
May 30		1		
May 31		1		
June 1		4		
June 2		3		
June 3				
June 4		2		
June 5		2	3	
June 6	1	1	1	
June 7		1	2	
June 8			2	
June 9			4	
June 10			2	1
June 11		3	7	5
June 12		1		8
June 13				5
June 14			1	
June 15				4

Samples of the catches taken during this period (table 16 and fig. 15) indicate considerable differences in size composition of the schools. Throughout the period there are two modes located at about 40 and 46 centimeters, respectively, but the relative numbers of fish in those modes shift from nearly equal representation in the early days to a marked preponderance in the 40-centimeter mode in the late days of the period. Moreover there are changes within these modes, the modal length in the 40-centimeter group shifting downward and in the 46-centimeter group shifting upward.

This, I believe, indicates (1) that in 1926 there was a mass movement of mackerel northeasterly

TABLE 16.—*Sizes of mackerel taken by purse seines along the Nova Scotian coast in the spring of 1926*

[Periods May 30 to June 2, June 4, to 9, and June 10 to 15 are represented by samples of 6, 13, and 29 catches, respectively]

Length in centimeters	May 30–June 2		June 4–9		June 10–15	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
36.0					1	0.1
36.5					1	.1
37.0			1	0.2	4	.4
37.5			2	.4	4	.4
38.0	1	0.2	5	.9	18	2.0
38.5	2	.5	12	2.2	38	4.2
39.0	8	1.9	24	4.4	73	8.1
39.5	11	2.6	52	9.6	136	15.1
40.0	24	5.7	71	13.1	164	18.2
40.5	36	8.6	81	15.0	154	17.1
41.0	35	8.3	89	16.5	115	12.8
41.5	26	6.2	38	7.0	51	5.7
42.0	18	4.3	25	4.6	33	3.7
42.5	15	3.6	17	3.1	12	1.3
43.0	12	2.9	11	2.0	6	.7
43.5	13	3.1	8	1.5	1	.1
44.0	22	5.2	5	.9	5	.6
44.5	25	6.0	7	1.3	8	.9
45.0	28	6.7	14	2.6	6	.7
45.5	24	5.7	16	3.0	4	.4
46.0	26	6.2	14	2.6	18	2.0
46.5	27	6.4	14	2.6	13	1.4
47.0	22	5.2	12	2.2	10	1.1
47.5	14	3.3	6	1.1	9	1.0
48.0	9	2.1	5	.9	2	.2
48.5	7	1.7	3	.6	4	.4
49.0	4	1.0	3	.6	2	.2
49.5	2	.5	2	.4	4	.4
50.0	4	1.0	1	.2	1	.1
50.5	3	.7	1	.2	1	.1
51.0	1	.2			1	.1
51.5	1	.2				
52.0					1	.1
52.5			1	.2		
Total	420	100.0	540	99.9	900	99.7

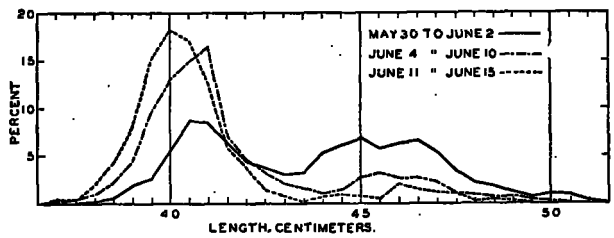


FIGURE 15.—Changes in mackerel population along the coast of Nova Scotia in the spring of 1926, as indicated by length-frequency distributions.

alongshore causing the fishery to shift in that direction, and (2) that schools from offshore (or from places not previously fished by the fleet from which our samples were taken) joined those already alongshore in sufficient numbers to change the size composition of the alongshore population. Inasmuch as the change in size composition took place in central Nova Scotia as well as eastern Nova Scotia and in the Canso region, the new schools joining those already there must have done so along a broad front extending from Halifax to Cape Canso.

TEMPERATURE CONDITIONS DURING THE SPRING MIGRATION

Mackerel of the southern contingent appear first at the place where the earliest rise in temperature of the water takes place.[22] This is consistent with older views such as that of Goode, Collins, Earle, and Clark who state (1883: 97) "their presence [in the open ocean] is nearly synchronous with the time when the water temperatures of the harbor [Woods Hole] have reached a weekly average of 45° (7.2° C.)." But a general correspondence of rise in temperature and appearance of mackerel proves no relation between the two for both are seasonal events and other elements of seasonal changes may be responsible. On the other hand, if there is a direct relation between the two, then the first appearance of mackerel should be early or late depending on whether vernal warming is early or late.

This appears to be true, since the first catches of the seasons of 1926, 1927, 1931, and 1933 varied as much as 10 days from each other (April 9–18), but varied only 2 days from the time that the temperature reached 45° F. (7.2° C.) at the Chesapeake Lightship in these respective years. The events in the other six seasons of the present investigation, with one notable exception, are not pertinent, because in these seasons the water at the Chesapeake Lightship had already attained 45° F. before the fleet arrived on the fishing grounds, and in all save the exceptional year, the first catches were made within several days of the arrival of the fleet, weather permitting. In 1932, however, during an exceedingly mild winter, the water did not cool below 45° F. (7.2° C.) until March 11 and was again up to 45° F. by March 21. Although the fleet arrived in the fishing area about the first of April, no mackerel were caught until April 15 after the water at the Chesapeake Lightship had stood at 50° F. for a week. Giving due weight to this striking exception, it must be concluded that temperature has a limiting rather than a causal influence on the appearance of mackerel. They are prevented from appearing in coastal waters before these warm to 45° F. (at the Chesapeake Lightship) but do not necessarily appear immediately upon attainment of this temperature.

The relation of temperature to the advance of the southern contingent along the coast may best be examined in the season of 1932 when oceanographic cruises at frequent intervals provided temperature observations on the mackerel fishing grounds during May and June (fig. 16). When first approaching the coast in April[23] (fig. 16, A) the schools of mackerel advanced shoreward as far as possible without entering water much cooler than 9° C., and in the first half of May (fig. 16, B and C) they advanced about as fast as did the 9° C. isotherm. After this time they lagged noticeably behind the progress of warming. Large bodies of mackerel remained in the vicinity of New York, where they were in water of 12° C. temperature, although they could have continued 200 miles eastward before reaching water as cool as 9° C. At the same time other schools were in a more easterly vicinity. These could have immediately pursued their northeastward journey, remaining in warm water by detouring slightly southeastward around the cooler Nantucket Shoals,[24] or they could have gone through the inner passage 10 days later.[25] Instead they remained around the edge of Nantucket Shoals, moving gradually around the periphery of the shoals, not reaching Massachusetts Bay until the end of June, though temperatures in the Bay rose to 9° C. before the middle of May.

To be sure, the lack of mackerel catches by vessels in May and the first half of June does not mean that some did not enter Massachusetts Bay during that period. On the contrary some were there by May 8, for mackerel were taken in a trap near Gloucester on that date; others were taken by pound nets at various points around the Bay during the remainder of May and during June. In all likelihood, these early arrivals were mackerel of the northern contingent, for in other years size-frequency distributions of mackerel from Massachusetts Bay in May and early June have always born greater resemblance to the northern rather than the southern contingent. Furthermore, the numbers caught were few in May and early June indicating that the southern contingent had not yet reached there.

[22] Although the 9° C. isotherm of early April 1930 in fig. 14 corresponds to the inshore limit of first catches, this particular temperature cannot have any significance because the catches are from many different years when the water may have been quite different in temperature.

[23] Since no temperature records were available in April 1932, temperatures and catches of 1929 were substituted. Although 1929 was a colder spring, the relation between location of catches and temperature is still evident, for both relate to the same year in each case.

[24] Whether they would have encountered temperatures much below 9° C. on Nantucket Shoals after May 25 cannot be said. The isotherms on fig. 16 were drawn on the basis of temperatures at the periphery of the shoal region and the minimum temperatures over the shoals proper is not known.

[25] Vineyard and Nantucket Sounds then were warmed to at least 10° C. as judged from temperatures at Pollock Rip Lightship situated at the eastern end of Nantucket Sound.

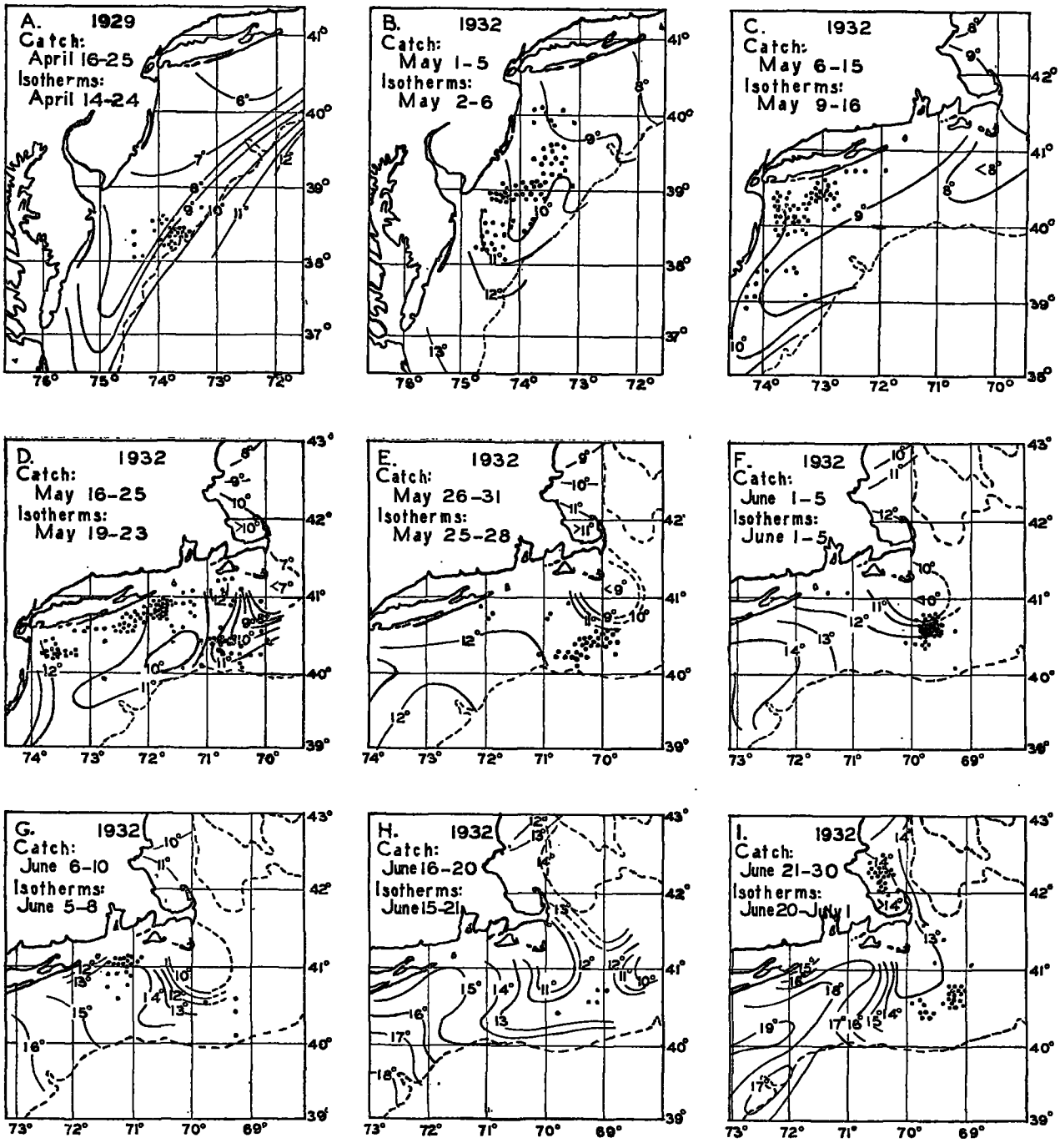


FIGURE 16.—Distribution of mackerel catches (shown by dots) during successive time intervals during the springtime in relation to surface temperatures (shown by isotherms for each degree centigrade).

It was not until June 10 that daily quantities as large as 1,000 pounds were taken in pound nets in any of the localities (representing more than 50 pound nets) of which records were available. Obviously, the southern contingent did not enter until late June when the vessel fishery shifted from the Nantucket Shoals region to Massachusetts Bay.

Beyond this point, geographically and chronologically, suitable temperature data are not available to pursue the relationship further, except to point

out that the surface waters of the entire Gulf of Maine usually become warm enough to be habitable to mackerel, from the temperature standpoint, by mid-June (Bigelow 1927, fig. 39, p. 574).

Comparison of surface isotherms and location of mackerel catches in other years are entirely consistent with the evidence of 1932 and it may be concluded that water colder than 7° or 8° C. forms a temperature barrier to northward advance of the mackerel, but the warming of the water to this point does not necessarily attract the fish along their northward migration.

RELATION OF FEEDING CONDITIONS TO SPRING ADVANCE

In American waters the mackerel is primarily a plankton feeder (Bigelow 1925: 202), consuming practically all members of the zooplankton except jellylike organisms such as medusae and ctenophores. From data given by Bigelow and Sears (1939), it appears that the waters along the spring migration route of the mackerel are well supplied with zooplankton from south of the offing of Delaware Bay in April to the offing of the south shore of New England in June. However, neither Bigelow and Sears (1939: 253–261, 268–270) in comparing distribution of mackerel catches with charts of nutritive plankton at richest level [26] in 1930, nor I in comparing the locality of mackerel catches with volumes of zooplankton in water stratum above the thermocline in several other years, could find a sufficient preponderance of instances wherein mackerel catches coincided with plankton concentrations to suggest that the mackerel tended to travel or tarry in waters richest in plankton content. However, if the feeding of mackerel reduces a zooplankton concentration rapidly and severely, one would expect an initially positive correlation between mackerel and zooplankton to become a negative one as feeding proceeds. Therefore this type of observation must remain indeterminate until much more is known about the dynamics of the situation. This need not prevent an examination of the relation of zooplankton and mackerel in more general terms.

During April, May, and at least a portion of June, in the area traversed by the mackerel, Bigelow and Sears (1939: 214–217) found evidence of a diurnal vertical mass migration of the zooplankton, causing the shoal water stratum from surface to about 20 meters to contain much more plankton in the nighttime than in daytime.[27] By July, however, this migration upward into the shoal stratum at night is suppressed, and plankton in this upper stratum is as poor in the nighttime as in daytime.

Having previously seen that the mackerel, while it is in continental-shelf waters, is a near-surface fish, probably confined to waters above the thermocline, it follows that feeding conditions become poor for the mackerel south of Cape Cod by July, for the plankton, even though persisting in this area, keeps to waters at or below the thermocline and, for the most part is inaccessible to the mackerel. Catches of mackerel are seldom made in this area after late June when the surface stratum becomes poor in plankton. While it is possible that some might stay, and that they might find subsistence by keeping to the deeper levels, in most years there is no evidence that any do.

There are, however, exceptional years when the main body of mackerel, as judged from the catch locations, does not depart on schedule. In 1928 and 1931 some mackerel catches continued to be made south of Cape Cod through July, and in 1936 the mackerel seiners continued to make catches there almost throughout the summer. Unfortunately, information is not available on plankton for this time of year in 1928 or 1936, but the surveys reported by Bigelow and Sears include 1931. Their summaries suggest that July of 1931 was particularly outstanding for plankton abundance at the north end of the area below Cape Cod. Their values for the whole column were 782 cubic centimeters [28] in that year as compared with 448 cubic centimeters and 285 cubic centimeters in 1930 and 1929, the only years available for comparison (loc. cit. p. 200).

Furthermore, there seemed to be a lesser tendency for the plankton to be confined to the deeper layers in that year. Whereas in July 1929 the ratio of

[26] All zooplankton except jellylike organisms such as ctenophores, medusae, or salps, was taken as the nutritive portion, and at stations where hauls were taken at several depth levels, the volume of the haul with largest catch was selected.

[27] In this connection it is interesting to note that purse seine fishing for mackerel at this season of the year is done at night whereas in later months it is done in the daytime.

[28] The quantities of plankton reported by Bigelow and Sears (1939) are given in terms of cubic centimeters of plankton per 20-minute towing with a 1-meter net. The speed of towing was judged to average 1.2 knots. Tows were horizontal at several different levels at each station in 1929 and oblique through several different strata in subsequent years. The "whole column" quantity is the mean of the catches at the several different levels or strata. While Bigelow and Sears do not claim the accuracy attending the straining of a measured amount of water, registration of flow past a current meter in the mouth of the net for 130 of these tows made under my supervision in 1932 indicated that the net strained an average of 456 cubic meters of water per 20 minutes of towing. Thus the statistics of Bigelow and Sears may be translated to the basis of cubic centimeters of plankton per cubic meter by multiplying them by a factor of 0.00219.

deep[29] to surface volumes for both day and night hauls was approximately 8 to 1, in July 1931 it was only approximately 5 to 1. The hauls were not strictly comparable for the 2 years, having been made horizontally in 1929 and obliquely in 1931, and so do not conclusively prove that plankton was more abundant in the strata accessible to the mackerel in 1931. The direction of change on both bases of comparison—total volume and relative proportion in the surface layers—suggests that the plankton may have afforded richer feeding in 1931, when mackerel stayed in the area through July, than in other years of record such as 1929 and 1930.

Although there are exceptional years, such as the ones just discussed, the fact remains that the main bodies of mackerel usually appear in the southwest portion of the Gulf of Maine between May 20 and June 20 and so have departed from the area south of Cape Cod well before its surface waters have been impoverished. They arrive in the Gulf of Maine at a time when zooplankton feed is rich there, where, according to Bigelow (1928: 45), copepods "reach their high-water mark early in June and other forms follow somewhat later."

Having reached the Gulf of Maine the southern contingent of mackerel has completed its spring migration. Although this is not true of the northern contingent, the lack of plankton records along Nova Scotia at times and places suitable for examining feeding conditions along the route of this contingent's migration prevents further pursuit of the subject.

On the whole, we have seen that plankton is relatively abundant along the route of the mackerel's spring migration at the time it takes place. It will be recalled from the section on food that during the months of the migration the fat content of the mackerel is increasing (table 2) thus proving that these relatively high abundance levels of zooplankton furnish good feeding. While there is no evidence that local mackerel and zooplankton concentrations tended to coincide with each other, the agreement of plankton abundance and the presence of mackerel in general suggests that evolutionary processes have brought about a habit pattern in which this species reaches various areas along its route of spring migration at a time when, on the average, feeding conditions are favorable.

[29] For the deep stratum in 1929 the hauls centered at the 10- to 30-meter level and in 1931 they centered at 20–30 meters.

RELATION OF SPAWNING TO THE SPRING MIGRATION

It has long been known that mackerel, when they approach the coast in the spring, are ripe or nearly ripe for spawning. But until the present investigation, simultaneous records of egg concentrations and mackerel catches were not available, and it was difficult to deduce the relationship between migration and spawning. Bigelow and Welsh (1925: 207) were of the opinion that mackerel "do not resort to any particular and circumscribed breeding ground, but shed their eggs wherever their wandering habits have chanced to lead them when the sexual products ripen." As we shall see, the evidence now available indicates that the process is not haphazard, the southern contingent resorting to certain grounds and the northern to others, and, although some eggs are shed elsewhere than on these grounds, such spawning is trifling compared to the concentrations on the respective major spawning grounds.

Some few members of the southern contingent spawn immediately upon entering continental-shelf waters, for we have taken eggs from surface waters at the edge of the continental shelf off the Virginia Capes in mid-April (lat. 36°46′ N., long. 74°37′ W., April 18, 1929). Greater numbers spawn farther inshore when the population reaches the offing of Cape May, but the maximum spawning concentration for the southern contingent is in mid-May in the triangular bight between the New Jersey and Long Island coasts (Sette 1939: 158). The main body moves to this area fairly rapidly and after the peak of its spawning there (after mid-May), continues its journey in the direction of Nantucket Shoals in a much more leisurely fashion, especially when nearing the Shoals.

Members of the northern contingent reach the area off southern New England presumably from offshore at about the same time or a little earlier than the main body of the southern contingent. They leave this region much sooner, and they seem not to spawn here, such spawning as does take place in southern New England being no more than can be accounted for by late-spawning individuals of the southern contingent as it moves eastward to occupy this area. Furthermore, such few samples of mackerel (of sizes appropriate to be of the northern contingent) as were examined from this area when the northern contingent predominated, were not ripe. Upon leaving this area, a small

portion of the northern contingent goes around Cape Cod into Massachusetts Bay (p. 290) where they spawn in May and June. The major portion of the northern contingent crosses the Gulf of Maine to the coast of Nova Scotia, and, joined perhaps by others from offshore, quickly make their way along the coast toward the Gulf of St. Lawrence (p. 290). Despite the large population moving along this coast in June[30] practically no spawning takes place here.[31] Following the tremendous June run along the Nova Scotia coast is the peak of spawning in the Gulf of St. Lawrence, indicating that this is the principal spawning ground of the northern contingent.

Thus, it appears that the spring advance of mackerel toward and along the coast is a series of three spawning runs: First, an advance toward the coast in the offing of the Maryland-Virginia peninsula and northward to occupy the inner half of the continental shelf up to southern New England in April and May; second, a small run into Massachusetts Bay in May and June; third, a larger run impinging first on the south coast of New England but destined to follow along Nova Scotia and into the Gulf of St. Lawrence, reaching there during June, and spawning through July and to a lesser extent into August. In all instances, especially the third mentioned, the movement is rapid until the spawning ground is reached. Once spawning has been accomplished the further movements of the shoals are more leisurely, more random in nature, and seldom seem to involve the whole units of the population.

To regard the spring movements as something other than spawning migrations would not account for (1) the definite concentrations of eggs in the Delaware Bay-Long Island sector, in Massachusetts Bay, and in the Gulf of St. Lawrence, (2) the consistently poorer egg concentrations off southern New England despite the dense population of adults that pass this sector in the spawning season, (3) the very scanty spawning along Nova Scotia despite the abundance of mature mackerel in June, (4) the rapid passage of the various contingents along the coast until they spawn, and their more leisurely progress afterward. All this, however, is consistent with the theory that the spring migration is a series of spawning runs.[32]

Of course, to say that these are spawning runs implies that the mackerel are impelled by the spawning urge without explaining the mechanism by which the movements are directed. In fact, the directive influence guiding the migrations of fishes is unknown for most fishes, many of which perform extended spawning migrations and have been much studied.

On the other hand, it has become known in recent years that bird migrations are connected with the development of reproductive organs, and this appears to be associated with lengthening of the day, either directly or through its influence on the amount of activity.

If the lengthening of the day somehow causes gonad development in the mackerel, and this in turn sets up a process causing the mackerel to move northward (whereby the lengthening of the day is augmented by the earth's inclination), several peculiarities of the migration would be explained. In the first place, migration begins shortly after the spring equinox when days become longer than nights. In the second place, the movement is as nearly northward as topography permits. In the third place, the only notable pause by a migrating group is the one which occurs when the northern contingent approaches the coast of southern New England where it is completely blocked in the northerly direction by the west to east trend of the coast line, and also for a time is partially blocked in the easterly direction by the cold water overlying Nautucket Shoals; rather than turn southerly to detour this cold water area, the contingent seems to wait until further warming erases this barrier. Finally, their taking a westerly (if not southwesterly) trend into Massachusetts Bay when the tip of Cape Cod is reached and into the Gulf of St. Lawrence when the north coast of Cape Breton Island is reached in June nearly coincides with the summer solstice when the lengthening of the day ceases and shortening begins. If this means a weakening of the impulse to move northerly they would be free to go in any direction. Actually, they turn westward where the water is, on the average, warmer.

Against this hypothesis is the fact that in Europe

[30] June catches comprise more than half of the annual take of counties along the coast of Nova Scotia (Sette and Needler 1934: 33).

[31] The data on spawning in Canadian waters are drawn largely from Dannevig 1919, and Sparks 1929, and have been discussed in detail by Sette 1943.

[32] To be sure, there is some scattered spawning wherever mackerel are found in the spawning season and, before the major concentrations of spawning in Massachusetts Bay and in the oceanic bight between the New Jersey and Long Island coasts were made known by this investigation, it was natural to suppose that the spawning was more or less at random.

a portion of the mackerel are known to winter in the deeper waters at the edge of the Norwegian Channel in the North Sea, and if these are of the same population that are caught in spring or summer around the British Isles or along the coasts of Sweden and Denmark, their movements in spring could not very well be northerly in direction. More must be known about the physiological responses of mackerel to various stimuli before this version of the migratory impulse can be anything but a hypothesis.

SUMMER SOJOURN

After the spring migration is over, the mackerel of the northern contingent have passed beyond the present-day range of the United States fishing fleet and the data of this investigation therefore pertain only to the southern contingent's summer habitat.

The region lying south and west of Cape Cod appears to be spawning ground rather than a summering place. Although every year a few mackerel, mainly young ones, remain scattered along the shores from Long Island east to Nantucket Shoals and are caught in pound nets in small, irregular quantities in every month of the summer, the main body after spawning moves in leisurely fashion eastward and around Nantucket Shoals into the Gulf of Maine. Usually they have passed the Shoals by July 1, but some years they linger later. In 1928 and 1931 some were there until July 31 and in 1936 the seiners continued to make catches in this region almost continuously through the summer.

The decline in abundance of plankton that takes place in the surface waters south of Cape Cod during the late spring months may be responsible for the departure of the main body of mackerel from this area at the end of June. In harmony with this idea is the previously noted (p. 294) instance of 1931 when plankton abundance was unusually high south of Cape Cod during July, and mackerel stayed there through the month, instead of proceeding to the Gulf of Maine.

During summer in all the years of this investigation, the catches of mackerel have come from the coastal zone and contiguous banks of the western half of the Gulf of Maine (fig. 17). A line drawn due south from Mount Desert Island to about 40 miles offshore and then paralleling the general trend of the coast line to Cape Cod, then eastward again to the sixty-eighth meridian and then south across Georges Bank would include on its western side all

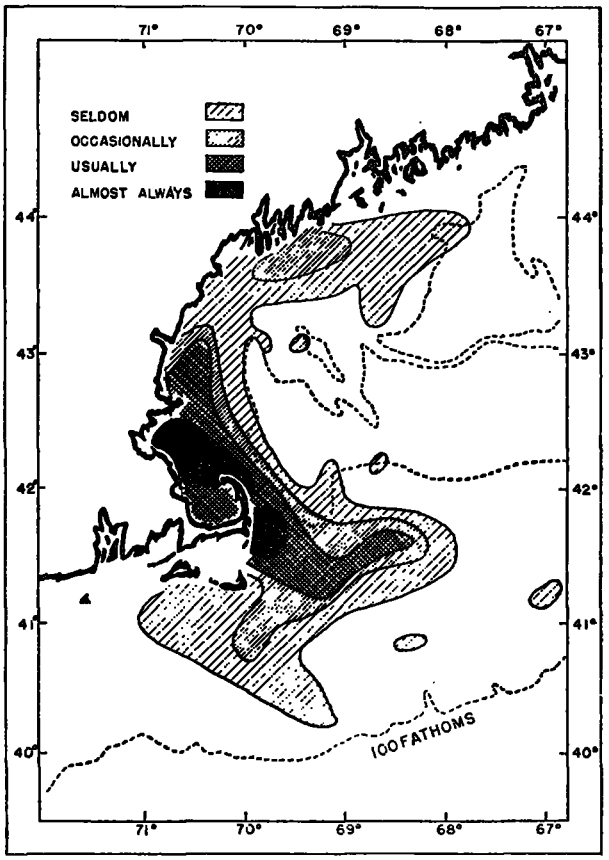


FIGURE 17.—Prevalent distribution of mackerel in the Gulf of Maine during July, August, and September, during the 10 years of investigation, as indicated by the number of seasons that catches were recorded from each 10-minute rectangle on the scale: "seldom," 1–2 seasons; "occasionally," 3–5 seasons; "usually," 6–8 seasons; and "almost always," 9–10 seasons during the period 1926 to 1935, inclusive.

but three catches of the many thousands whose location had been recorded during the course of the present investigation. This appears to be at variance with the opinion of Bigelow and Welsh (1925: 190), who reviewed records of sightings of mackerel schools and of catches from earlier years to conclude that "at one time or another the mackerel is practically universal in the Gulf of Maine, for not only does it appear in great abundance on the offshore grounds—that is, Nantucket Shoals, Georges and Browns Bank—and all over the central deeps, but also throughout the coastal belt; . . ." They mention in particular that in 1882 "vast schools were found over the offshore deeps of the Gulf between Georges Bank, Browns Bank, and Cashes Ledge and thence northward to within 40 miles or

so of the Maine coast . . ." However, occurrence in the middle portions of the Gulf must have been exceptional rather than usual even in these earlier years.

In reading through the many accounts of mackerel fishing and of the mackerel fishery published during the first several decades after establishment of the United States Fish Commission, one is impressed with the frequency in which fishing along the coast is mentioned, with the emphasis on the coastal nature of the fishery in the Gulf of Maine in summertime, and with the rarity of any really offshore records. In the season of 1885, when month by month accounts of the progress of the mackerel fishery were published (Wilcox 1885, 1887), the locations of fishing within the Gulf of Maine were so much like those recorded during the present investigation, that it is impossible to select any instance of significant difference.

Beginning with 1893, statistics, classified by fishing ground, were published on the landings at New England ports by the fishing fleet. The mackerel landings reported in this series were tabulated by Sette and Needler (1934: 27) for each year during the period 1893 to 1930. Out of a total of 260,662,000 pounds reported from the Gulf of Maine localities from 1893 to 1925, the only catches that could be classified as coming from the middle portion of the Gulf of Maine were those from Cashes Bank, which aggregated only 103,000 pounds or 0.04 percent of these 33 years of landings. During the next 5 years the percentage relationship is about the same; of a total of 160,135,000 pounds 37,000 or 0.02 percent came from Cashes Bank. Similarly for the first 33 years 18.7 percent were reported from Georges Bank and during the next 5 years 24.4 came from there. From the records of the present investigation we know that the catches during the 5 later years were practically all from the westerly end of Georges Bank and there is no reason to believe that those of the preceding 33 years did not come from the westerly end of the Bank also. In the earlier period also 6,886,000 pounds or 2.6 percent were reported from the Bay of Fundy. All of the remainder in both periods came from grounds classified as "New England Shore."

The 33-year period was prior to the present investigation and the 5-year period coincides with the first half of the investigation. In comparing the two periods, there is little to suggest that mackerel have occupied different portions of the Gulf formerly than they do now, excepting the Bay of Fundy catches. The latter were all landed in the years 1901 to 1906, suggesting that for a short time, only, a fishery was found profitable there. A similarly impermanent fishery was carried on in the Bay of Fundy some 30 years earlier, but was abandoned, apparently for lack of mackerel there after 1876.

In general, then, it appears that the 10 years considered here are not atypical, either of the mackerel's habits or of the mackerel fishermen's habits in most years, at least since purse-seine fishing became customary. While our series does not include such an exceptional year as 1882, or any series of seasons affording catches from the Bay of Fundy, and so cannot throw light on these unusual occurrences, they should serve well to represent the most usual pattern of the fishery's distribution during the summertime.

There is reason to believe that when the adult mackerel population consists mostly of the younger ages, the schools tend to stay relatively close to shore during summertime; when it is comprised mostly of the older and larger adults, the schools tend to range farther offshore. During the three summers beginning with 1926, the 1923 class dominated in the population of the Gulf of Maine. Hence, the average age and size of individuals composing the population increased steadily during this period, the modal lengths as of July being 38.2, 39.4, and 40.1 centimeters in 1926, 1927, and 1928, respectively. During these three seasons there were successively higher proportions of catches at offshore locations.

In 1926, all catches were made within 45 miles of shore; in the following year, 82½ percent of the catches were made within 45 miles of the shoreline and 17½ percent were made farther than 45 miles from shore; and by 1928, 33 percent of the catches were made farther than 45 miles from shore (table 17).

In 1929, the trend seemed to set back toward the shore line, only 26 percent of the catches being made more than 45 miles from shore. However, in this season the population consisted of two well-marked size groups. There were the large mackerel of the 1923 and older classes now grown to a modal length of 40.8 centimeters, and the yearling mackerel of the 1928 class having a modal length of only 27 centimeters (in July); and there were very few fish of intermediate sizes from the 1924 to 1927 classes. When the samples from purse-seine catches of 1929 in the Gulf of Maine are segregated according to the two size groups, more than 57 percent of the large-fish

samples proved to have been caught from beyond 45 miles from shore, whereas, less than 1 percent of the small-fish samples were from beyond the 45-mile zone. Thus the trend toward "offshoreness" of large fish continued through 1929.

TABLE 17.—*Distance from shore of purse-seine catches of mackerel during July to October, inclusive, 1926 to 1929*

Year	Percentage of mackerel taken at each 10-mile (nautical) interval of distance from shore							
	10	20	30	40	50	60	70	80
1926	66.0	29.1	4.1	0.7	------	------	------	------
1927	37.8	19.4	14.5	10.8	8.0	6.3	2.6	0.6
1928	37.8	9.2	9.8	10.2	8.2	18.4	5.1	1.3
1929	54.0	9.5	3.8	6.8	13.3	10.3	2.2	.2

It should be noted, however, that these offshore catches were confined almost entirely to the northwest portion of Georges Bank (area XXII H), none being made over the central deeps of the Gulf of Maine.

In the years since 1929 there has been a goodly supply of 1-, 2-, and 3-year-old mackerel in the population, and these afforded good catches in the inner coastal zone, so that it was not necessary for the fleet to go farther offshore to locate the larger sizes even though a greater market preference for the latter tended to counteract this inclination. Such of the larger sizes of mackerel as were present in the coastal zone near the western side usually were there only early in the summer immediately following the spawning season, thereafter, they disappeared from the catch, presumably going farther offshore than the fishing fleet cared to follow as long as the fishing on the smaller sizes alongshore proved successful.

In addition to the size-connected difference between inshore and offshore mackerel in the summertime, there is evidence also that the population is not homogeneous from north to south. Unfortunately, space does not permit inclusion of detailed frequency graphs of samples in small-area and short-time groups for the summer months. But the early fall period is an extension of the summer period during which the mackerel population apparently remains distributed more or less according to the summer pattern. Fortunately, examples of the lack of homogeneity now to be considered are evident in the graphs for early fall in the three seasons included in figure 11. In fact, they are so obvious that the reader may have questioned the implication in the section on the existence of contingents that each contingent is a unit population rather than an aggregate of several more or less discrete populations inhabiting different subareas. To a limited degree the latter is true as we shall see.

The differences in the early fall (September) length-frequency distributions of table 23 and figure 11, suggestive of nonhomogeneity between subareas can be grouped into two categories (1) slight differences in the position of the modes and (2) differences, usually slight, in the relative strength of the right-hand tail of the various distributions.

The first category is illustrated in the September 1926 distributions as a difference between subareas D and E on the one hand and G on the other. Since D is represented only by 40 fish out of the 2,900 measured during this month, it has been left out of consideration and the distributions simply of subareas E and G compared in pairs as given in table 18.

TABLE 18.—*Comparison of length-frequency distributions for September 1926 by the chi-square method with corresponding probability values*

Comparison	Chi-square	P
Area E with area G:		
Sept. 1–10	39.3	<0.001
Sept. 11–20	60.8	<.001
Sept. 21–30	38.3	<.001
Sept. 1–10 with Sept. 11–20:		
Area E	19.3	.05
Area G	21.0	.03
Sept. 11–20 with Sept. 21–30:		
Area E	19.77	.05
Area G	25.4	.008

It is seen that where the distributions from the same subarea in successive periods are compared, the chi-square value tends to be around 20 to 25 which, for the 11 degrees of freedom afforded by the 12 size-classes remaining after pooling the tails below 35.5 and above 40.0 centimeters, corresponds to probabilities between about 0.01 and 0.05. These results conventionally would be considered of significance or of border-line significance. But when account is taken of the theory underlying the chi-square distribution from which the probability value is derived in conjunction with the conditions under which these samples of mackerel were drawn, a conventional interpretation is questionable.

Although each of the frequency distributions here under consideration contains in the order of 500 individuals (240 to 600), this is not the equivalent of a set of 500 independent random drawings from a universe. Our individuals were drawn in subsets

of 20 individuals, 1 such subset from each cargo of mackerel. The cargo of mackerel in turn is usually made up of the catch of 1 school or sometimes 2 or 3 schools, but never as many as 20 schools. If, as there is reason to believe, the mackerel tends to assort into schools according to size of individual (p. 264), we no longer can regard a set of 500 fish made up of 25 subsets as 500 fully independent drawings and we should expect the tabular values of P to be fictitiously low.

However, if the number of individuals per sample, the tendency of assortment by sizes in the schools, and the variance of the general population which is assorted into schools all remain approximately the same as between sets of data to be compared and if the data are partitioned into size classes affording identical number of degrees of freedom for each set, then the relative values of chi-square or of its corresponding probability may be of significance. In all probability these conditions are either exactly or approximately met in the several frequency distributions listed in table 18. Furthermore, it probably is consistent with all known facts to regard a chi-square value of 20 to 25 between these particular pairs as indicating no real difference in the populations sampled.

Turning now to comparison of distributions for different subareas during the same time period, the chi-square values are 38 or higher and corresponding probabilities are less than 0.001. Whatever the limitations of the chi-square method as applied to these data, there can be no doubt that the samples of subarea E differed more from those of subarea G than did the samples taken during successive time intervals within each subarea. Adding to this evidence the fact that the displacement of the mode in E as compared with G is consistently in the same direction, the evidence is substantial that the distribution of mackerel by sizes was not homogeneous as between subareas.

For summers and early fall of other years such small but doubtless significant differences between the frequencies of sizes of mackerel from well-separated areas of fishing are sometimes detectable from inspection of the frequency graphs and sometimes not. The suggestion therefrom is strong that during the summer period the mackerel population may become segregated between several fishing grounds and remain so for several weeks to a month or more at a time.

I have noted no instance where such segregation has persisted during the entire summer and early fall. In 1926, for instance, though the segregation was plain during September, there was little evidence of it during the preceding August. In 1927, on the other hand, it was well marked as between subareas F and G during a part of August, but at that time there were only a few catches from subarea F and later they ceased completely. The segment of the population in subarea F may have been a small one that later joined with the probably larger populations in E or G in which their relatively small numbers would be undetected.

On the whole, these segregational events seem irregular and temporary, indicating certainly a lack of complete mixing of the main population at all times during summer but not indicating the existence of stable independent units.

The second category of nonhomogeneity is illustrated by the frequency graphs for September of 1927 in figure 11. The frequencies from subarea E have a long "tail" extending to the right which is much more pronounced than the tail extending to the right in the frequencies from subareas G, H, O, and P. Taking the sum of the individuals whose lengths exceed 41.25 centimeters as the tail of the distributions, and pooling all September data, it is found that the distributions from subarea E have 48 out of 320 or 15 percent of the individuals in the tail, whereas those from G, H, O, and P have only 123 out of 2,210 or 5.6 percent in the tail. Treating the four counts given in the preceding sentence as a 2 by 2 contingency table, the chi-square value is 43.5 which corresponds to a probability of far less than one in a thousand that such a divergence in the tail portions could occur by chance. Part of this difference may be attributed to the nonrandomness of the several samples comprising each set of data, as was above discussed at length. But the very high chi-square value suggests that the difference is real. Even a greater weight of evidence is provided by the fact that the mackerel-lengths comprising the tails of the distributions from subarea E cover approximately the range of lengths that are present in the entire distributions of what has been recognized as northern contingent, as exemplified in the December frequencies of the same year.

In fact, it is possible to examine the question: Is the distribution of individuals among the size classes in the tail on the distribution from area E consistent with the hypothesis that the tail consists of an admixture of northern contingent mackerel

such as were caught in December with southern contingent mackerel such as were caught in subareas G, H, O, and P in September? We have given as our empirical distribution, 320 fish from area E in September, of which only the frequencies in the right-hand tail above 41.25 centimeters are of interest. These comprise 48 fish. Our hypothesis is that these 48 fish are distributed as if they were combinations of 2 populations: (1) Southern contingent mackerel for which the model distribution is the set of samples containing 2,210 fish from areas G, H, O, and P for the month of September, and (2) Northern contingent mackerel for which the model is one set of samples containing 800 fish from drift-gill-net catches from area E during December 11 to 20. These will be called populations I and II, respectively. Population I has 123 fish and population II has 667 fish above 41.25 centimeters. The proportion of population I to population II in the combination is not included in the hypothesis and must be determined empirically.

If we let x_1 be the numbers of fish to which population I should be weighted and x_2 be the numbers of fish to which population II should be weighted, then

$$x_1+x_2=320$$

will satisfy the requirement that the theoretical population will have the same number as the observed population, and

$$\frac{123}{2{,}210}x_1+\frac{667}{800}x_2=48$$

will satisfy the requirement that the theoretical population will have the same number of fish as the observed population in the segment of the tail lying above 41.25 centimeters. Solving the two simultaneous equations we find that the frequencies of population I should be weighted to total 281.2 fish and those of population II to total 38.8. Combining these two populations so weighted we may examine the tail portion above 41.25 centimeters to see whether the distribution of fish among the several class intervals is sufficiently similar in both the theoretical and the observed population to be consistent with the hypothesis that this tail of the latter distribution could be composed of an admixture of northern with southern contingent fish.

In applying the chi-square test, it is necessary to combine several of the half-centimeter class intervals to contain a minimum of five individuals per new class-interval (in the theoretical distribution). After this is done there are seven class-intervals with a total chi-square of 9.0; entering the table with 6 degrees of freedom, the probability is 0.17 that the difference between the two curves could have arisen by chance. Thus, within the limitations of sensitivity of the test, which, with only 48 fish, distributed in seven size classes, is not very great, the hypothesis that the area E samples contained northern contingent fish in the tail is consistent with the data.

Indications, similar to the above, of admixture of some northern contingent mackerel with the predominently southern contingent mackerel in the northwesterly portions of the Gulf of Maine are evident, not only in the 1927 material, but occur practically throughout the summer mackerel frequencies of all 10 years of the series. Frequencies from subareas C, D, E, and F, all north of Cape Cod, contain, in the size classes appropriate for northern contingent mackerel, an excess of individuals over the relative number found in these size classes among the mackerel taken contemporaneously in subareas G, H, O, and P, all east and south of Cape Cod. More rarely, there are groups of samples taken, usually in the northwestern part of the Gulf of Maine, which have size compositions nearly identical with that of the northern contingent mackerel as it is found in the spring off Nova Scotia or in the late fall off Massachusetts.

It appears to me, therefore, that there must be a small segment of northern contingent mackerel that stays in the Gulf of Maine throughout the summer, that this segment is small relative to the southern contingent present in the summer, and that this small segment generally keeps well north of Cape Cod.

In some seasons there has been a tendency for the distribution of mackerel catches as a whole to be more northerly than in others. The years 1926, 1927, and 1933 to 1935 were examples of southerly distribution wherein practically all of the catches were made in Massachusetts Bay or southward (fig. 18). During the years 1929 to 1933 a much larger proportion of the catches were made north of Cape Ann (fig. 19). It may be significant that the southerly distribution was most marked during the years when the 1923, 1930, 1931, and 1933 classes were dominant; whereas the northerly distribution was confined to the years when the 1927, 1928, and 1929 classes were dominant. The first-named group of year classes were predominantly members of the southern contingent even in their later years, while the last-named group appeared to have joined the

northern contingent after attaining appropriate ages. It is possible, therefore, that year classes destined eventually to be northern contingent members, may presage this event by exhibiting a tendency toward northerly summer distribution some years before they actually join the extensive northerly spring migration of the northern contingent.

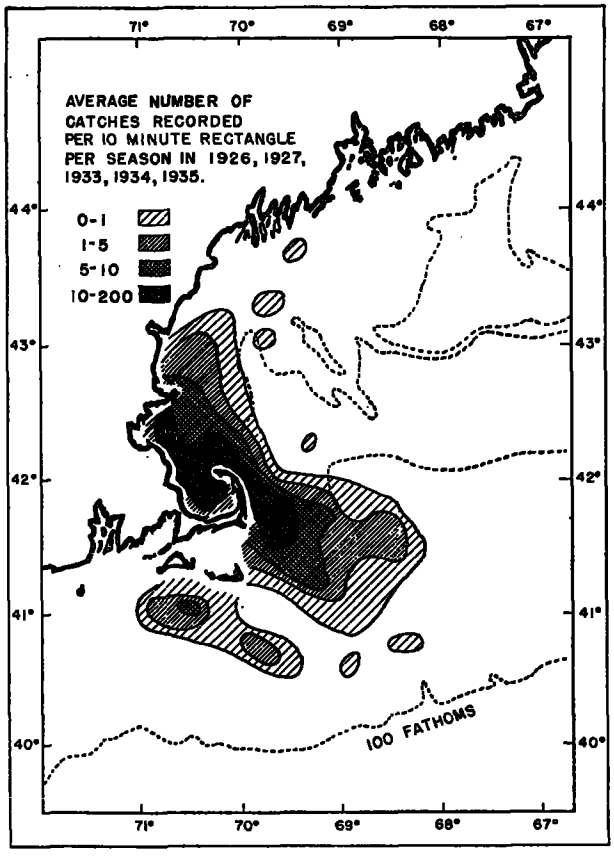


FIGURE 18.—Relative concentration of mackerel schools in 1926, 1927, and 1933–35 during the months of July to October, inclusive, as indicated by the average number of catches made per 10-minute rectangle per season by purse-seine vessels.

INFLUENCE OF FEEDING CONDITIONS ON MOVEMENTS OF THE MACKEREL IN SUMMERTIME

Regarding the feeding conditions encountered by mackerel and the effects of distribution of planktonic feed on the distribution of mackerel during their summer sojourn in the Gulf of Maine, there is a regrettable paucity of information on plankton that is suitable for drawing conclusions. Bigelow's (1926) data are for years not covered by my records of mackerel distribution. They demonstrate that the plankton is richer in the Gulf of Maine generally

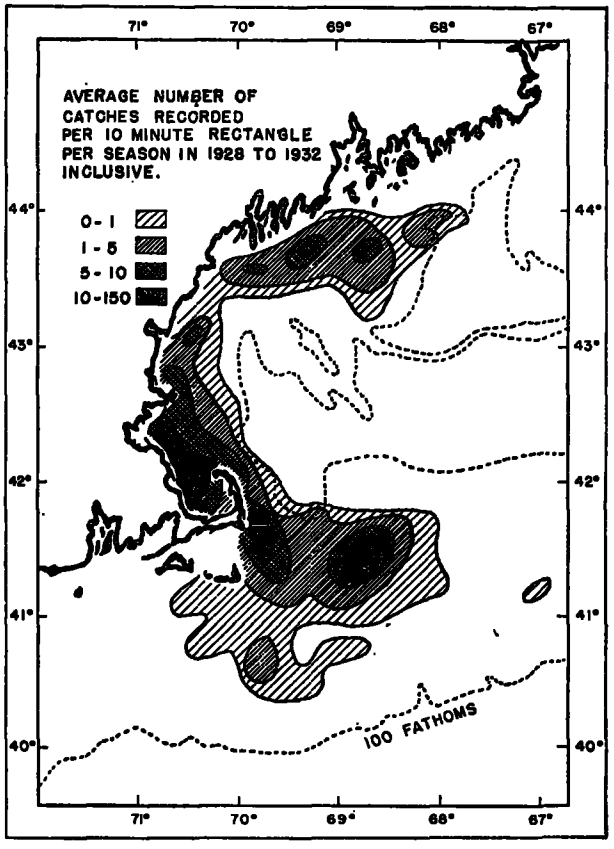


FIGURE 19.—Relative concentration of mackerel schools during July to October, inclusive, during the years 1928 to 1932, inclusive, as indicated by the average number of catches made per 10-minute rectangle per season by purse-seine vessels.

during the summer period when the mackerel catches are also taken mainly in the Gulf of Maine, but do not indicate whether it is richer in the parts usually frequented by the mackerel than in other parts. In fact, his quantitative hauls for the summer period (Bigelow 1926: 86) show the richest band extending from southwest to northwest directly across the Gulf of Maine with only its southwesterly extremity coinciding with the area customarily yielding mackerel catches. Also the alongshore area north of Cape Ann where mackerel are caught in abundance in some years gave the lowest plankton volumes. This apparent lack of correspondence between richness of plankton and mackerel catching grounds may however be entirely without significance because Bigelow's quantitative hauls were drawn vertically from near bottom to surface and portray the aggregate plankton population rather than the concentration in the surface layers inhabited by the mackerel.

Similarly Redfield's (1941) quantitative study of plankton in the Gulf of Maine was based on vertical hauls through the entire water column and was not particularly suited for the solution of the problem here considered. After examining my charts of mackerel catches in relation to his plankton volumes, Redfield was able to conclude that "It seems sufficiently clear that in early summer mackerel are available chiefly along the southern shores of the Gulf, that by late summer their abundance has shifted to the northern shores, including the Bay of Fundy. This is the distribution of the maximum of zooplankton population as well." Beyond this generalization that the sequence from south in early summer to north in late summer in both plankton and mackerel distribution, it is not possible to see any striking correspondence between the two on the basis of the Redfield data.

The charts of plankton distribution given by Redfield cover periods either rather early or rather late in the summer period. In the period of May 21 to June 3, 1934, the plankton-rich zone, as shown by the area included within the 50 cubic centimeters (per square meter of sea surface) contours, extended from abreast the Massachusetts Bay-Cape Cod-Nantucket Shoals sector in an easterly direction across the Gulf of Maine. Mackerel catches at that time were mostly (65 percent) west of Nantucket Shoals and so not within Redfield's survey area. The remainder were from statistical area XII–O, at the very southwesterly corner of the survey area, and it is not clear whether any were within the plankton-rich zone. From an extrapolation of the isometric lines representing plankton distribution, it appears likely that only a part of these mackerel catches could have been within the plankton-rich zone.

In the period September 2 to 14, 1933, the plankton-rich zone, as judged from the 50 cubic centimeters contour, covered the westerly portion of the Gulf of Maine, its westerly boundary lying well offshore, averaging perhaps 40 miles from the coast. A plankton-poor area with less than 25 cubic centimeters seemed to border the entire western shore line. All the mackerel catches for the month of September 1933 were made in Massachusetts Bay and close in to Cape Ann; thus the mackerel were well inshore of the main zone of plentiful plankton and in water that was very poor in plankton, unless there was a local plankton concentration within Massachusetts Bay. Redfield's survey included no stations within the Bay, though there was one at the tip of Cape Cod which should have reflected any richness of the Bay because the circulation pattern is such that water usually flows out of the Bay past this station. Since only 3 cubic centimeters were taken at this station, it hardly seems that the Bay could have been very rich in plankton at this time.

In the period of September 17 to 27, 1934, the plankton-rich zone lay obliquely across the Gulf of Maine, extending roughly from southwest to northeast and mostly over the central deeps. Mackerel apparently were confined to the westerly borders of the Gulf. Of 225 mackerel catches during September 2 to 29, 1934, inclusive, 204 were in Massachusetts Bay, which was not sampled for plankton in the Redfield survey of September 1934. Of the remaining 21 catches only three were in the zone of plankton yielding more than 100 cubic centimeters drained volume of plankton per square meter of sea surface, 7 were in the 50–100 cubic centimeter zone and 12 in water yielding less than 50 cubic centimeters per square meter.

This apparent lack of agreement is perhaps what would be expected from the nature of the organisms concerned and from the type of data upon their occurrence. It has been pointed out that mackerel probably keep to the waters above the thermocline and the latter is often only 20 meters below the surface and seldom more than 50 meters below. Furthermore, the evidence on the distribution of mackerel is the location of fishermen's catches which are made only at or near the surface. Zooplankton, on the other hand, occurs at all levels from surface to bottom and the evidence on its relative abundance was from vertical hauls which represent the total quantity from surface to sea bottom rather than the concentrations in the upper levels. According to Bigelow (1926: 28) there is a decided cleavage in the plankton community between the upper and lower levels with the 100- to 150-meter level roughly delimiting the two. Accordingly, the vertical hauls in deeper portions of the Gulf of Maine draw on plankton populations in addition to those that either remain in near-surface levels or migrate into and out of them diurnally as does the important calanoid community (Bigelow 1926, p. 24; Clark 1934a, p. 430, 1934b, pp. 436–444). The inclusion of the deeper plankton in the vertical hauls would make the plankton appear to be relatively rich over the central deeps of the Gulf of Maine, when in fact the

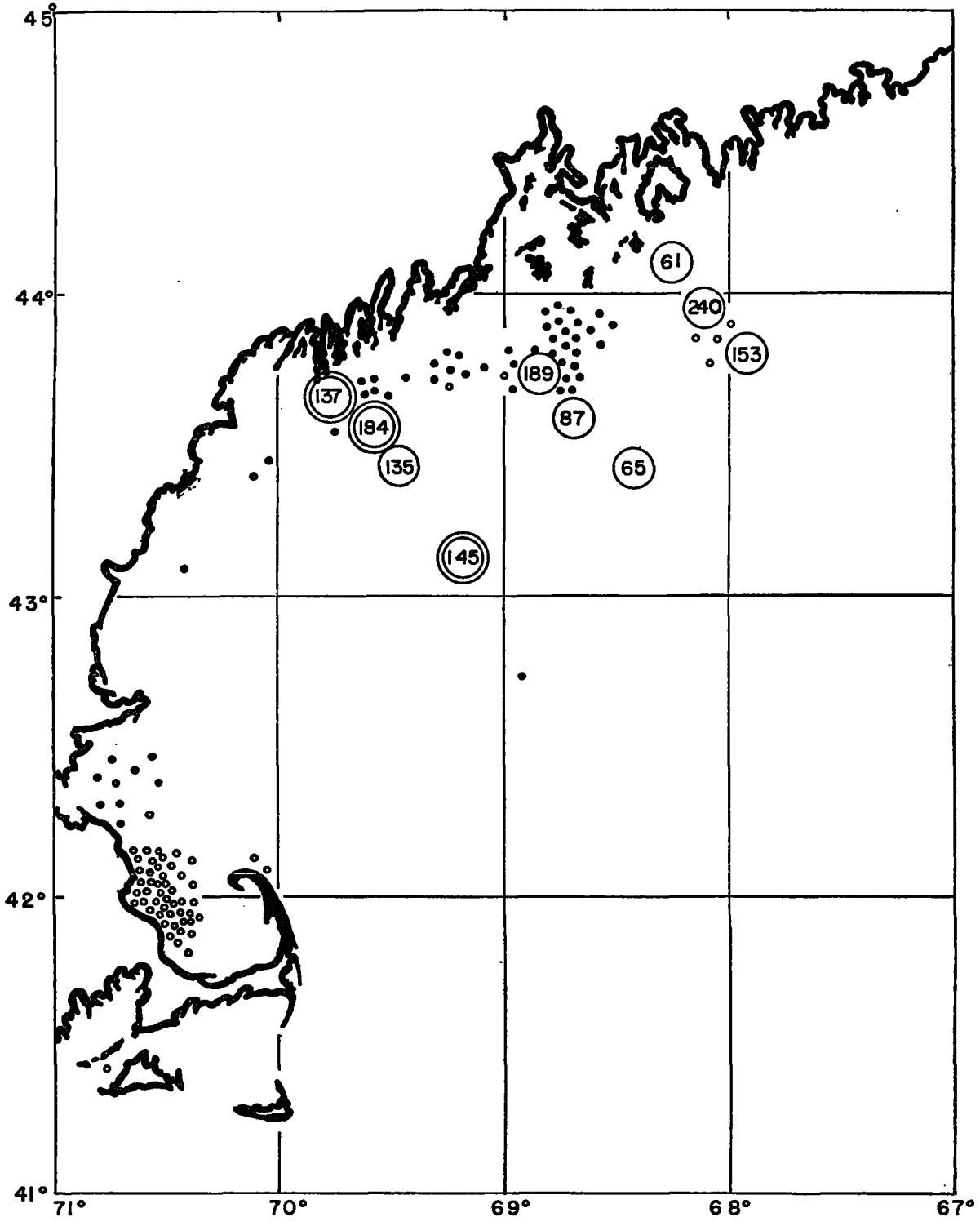


FIGURE 20.—Distribution of mackerel catches and of zooplankton in the upper 50-meter stratum of the waters of the Gulf of Maine in late August 1932. Solid dots indicate catches of large, and small, open circles catches of small, mackerel during August 6 to 20, 1932. Large circles indicate the position of the plankton hauls, and the numbers in them give the quantity caught, in centimeters (by displacement), per 20-minute oblique tow with a meter net from 50 meters to the surface. Double circles indicate that more than 30 percent of the plankton, by number, consisted of euphausids.

plankton in upper layers inhabited by the mackerel might really be much poorer over the central portions of the Gulf than along its borders.

To properly investigate the relation between feeding conditions and the mackerel's distribution in the summertime would require a quantitative sampling of that portion of the plankton which is available to the mackerel. This would likely include all of the forms living continuously in the layer above the thermocline and also those forms which may be found below the thermocline in the daytime but migrate upward nightly to or through the thermocline as Calanus (Clark 1934a, 1934b) sometimes does. The results of such sampling should moreover be available for the same period of time as is covered by the information on mackerel distribution.

Despite the fact that the Gulf of Maine probably is the most-studied portion of the sea adjacent to North America, I have been unable to find data that meet this specification. Most nearly approaching it are data on a group of hauls reported by Fish and Johnson (1937). For present purposes, as published, they have the fault of including plankton bathymetrically unavailable to mackerel, for the catches of hauls traversing the layer from 50 meters to the surface were combined with the catches of hauls traversing the layer from bottom to the 50-meter level. However, Dr. Charles J. Fish kindly furnished me his measurements of volume in terms of cubic centimeters of plankton, drained measure, caught in 20-minute oblique hauls drawn from 50 meters to the surface. They were taken mostly in the daytime and may not fully represent the calanoid community. The values have been plotted in figure 20, to which have been added the locations of mackerel catches during nearly the same period of days as was covered by the plankton survey.

Unfortunately, the area covered by the plankton survey does not extend far enough in a southwesterly direction to include the entire fishing area. The sector along the coast of Maine was sampled by Fish and Johnson, and also afforded mackerel catches. In this sector the plankton tended to be most concentrated in a zone paralleling the coast and lying about 15 to 25 miles offshore. The mackerel catches are concentrated along approximately the same zone. Giving due consideration to the fact that the time periods for mackerel and plankton catches are not identical and that the plankton catches may variously underrepresent or overrepresent the calanoid community, depending on where its vertical migration brought it in relation to the 50-meter level at the particular time each haul was made, the agreement is very good.

This suggests that mackerel may, during their summer sojourn, keep to areas that provide the richest feeding. Alternatively, it suggests that they are most accessible to the fishermen in such areas. In either case, some of the great differences in the distribution of the mackerel catches within the Gulf of Maine during some seasons as compared with other seasons might prove to be due to unusual variations in the plankton production cycle and in the distribution of the plankton community. Surveys designed expressly to test this possibility might have fruitful results, not only in elucidating the ecological complex of which the mackerel population is a part, but also in the discovery of causes of apparently anomalous fluctuations in the success of the mackerel fishery.

All of the above discussion is based on the premise the zooplankton is the basic feed of the mackerel in the summertime. There is the possibility, also, that small fish and other relative active forms may be important in the ration of the mackerel (p. 268). This possibility needs investigation. If found to be true, there would be a further interesting possibility. Small fish used as feed by the mackerel, in turn feed upon the plankton. If such small fish are tolerant of a wider range of temperature than the mackerel and so free to feed below the thermocline as well as above it, they could, in effect, constitute a food link between the deeper plankton community and the near-surface mackerel.

FALL DEPARTURE

Little can be added to the information already extant concerning the autumn movements of that portion of the mackerel population inhabiting Canadian waters in the summertime, except to point out that although some mackerel remain there until late in the fall (to the end of November), statistics on the monthly catch in the various portions of Canada (Sette and Needler 1934: 34) indicate that the fall run of mackerel is heaviest along the shores of Prince Edward Island in September and along the southeastern shore of the Gulf of St. Lawrence and the coasts of Cape Breton and Nova Scotia in October. Presumably this peak in the catches marks the passage of the main body of northern contingent mackerel along these coasts on its departure from waters north of the Gulf of Maine to go to its winter habitat south of the Gulf of Maine. The small

portion of the northern contingent that winters along the edge of the continental shelf off Nova Scotia apparently lags behind the main body in leaving Canadian shores. This is suggested by the small catches made off Nova Scotia after October.

South of Canadian waters there is more detailed evidence available on the time of fall departure. Typical of this evidence are the frequency graphs included in figure 11. In 1926, the population in the Gulf of Maine continued to have typically southern-contingent characteristics, its frequency distribution being unimodal with modal length at 38 centimeters, until October 15. Thereafter, it changed sharply to a modal length of 40.5 centimeters among the mackerel caught by seiners, and subsequently shifted upward to 41 or 41.5 among the mackerel caught by fishermen operating drift gill nets (known locally as "netters"). These sizes, obviously characteristic of northern-contingent mackerel, undoubtedly indicated the incursion of the latter group into the Gulf of Maine, where they replaced the southern contingent as it withdrew from the Gulf of Maine in the middle of October.

The change is not always abrupt. In the following year, 1927, purely southern-contingent mackerel with a modal length of 39 centimeters were in samples from the Gulf of Maine until October 8. But these were joined by northern-contingent mackerel in the latter half of the month causing multimodal size composition with one mode indicated at 39.5 and another well-pronounced at 41.5 centimeters. By the end of October, however, the southern contingent had gone, leaving practically no fish at the former modal length of 39 or 39.5 centimeters. On the other hand, the northern-contingent mackerel with their modal length at 41.5 or 42 centimeters made up the entire catch after November 1st and continued to furnish fishing to the netters until the middle of December.

In some years the late summer and fall samples show traces of that minor portion of the northern contingent which is presumed to stay in the Gulf of Maine instead of migrating to Canadian waters as the major portion is supposed to do. Late in August of 1928, while a population with modal length of 40.5 centimeters, obviously of the southern contingent, was found in the offing of Cape Cod (areas XXII–G and H, August 22 to 29), another population with modal length at 42.5, obviously northern contingent mackerel, was in the northern part of the Gulf of Maine (area XXII–C, August 23 and 24). Early in September these northern-contingent mackerel had moved down to Massachusetts Bay, judging by the size composition of 60 mackerel from area XXII–E, September 6 to 10. Some of them had filtered past Cape Cod to join the southern contingent still present in areas XXII–G and H, causing a pronounced skewing toward the right of the length-frequency curves for middle and late September. During the ensuing days of September, this hump persisted, indicating that northern- and southern-contingent mackerel were mixed in the offing of Cape Cod. Early in October the fishery shifted from the offing of Cape Cod to the offing of No Man's Land, i. e., southwestward past Nantucket Shoals. Here the population contained fewer mackerel in the 42–47 centimeter range and it is possible that the northern-contingent mackerel which were in the offing of Cape Cod early in September did not follow to the main body to the vicinity of No Man's Land. Unfortunately, the number of samples is hardly adequate to demonstrate this beyond doubt.

After an interval of time, large numbers of mackerel appeared in the offing of Cape Ann, where they became the object of the drift-gill-net fishery during the last few days of October, all of November, and the first half of December. Judging from the sizes of fish and their abundance, these must have been the main body of the northern contingent that had reached the western part of the Gulf of Maine on its return from waters off Canada.

Further examples might be drawn from other years, but the three given are sufficient to show the course of events, and when considered together with the monthly catch statistics, give a fairly complete report of the autumn withdrawal. According to this evidence, the southern contingent departs from the Gulf of Maine during October, at the same time as the northern contingent is leaving Canadian waters. At least a portion of the northern contingent, on leaving Canadian waters, passes through the Gulf of Maine, and it is this population in transit past Cape Ann that furnishes material for the drift-gill-net fishery in late October, all of November and early December. In passing through the Gulf of Maine, the earliest of the northern-contingent mackerel sometimes mix with the latest of the southern contingent, which have not left the Gulf of Maine by the time the northern contingent arrives there.

On leaving the Gulf of Maine, the southern contingent goes out by way of the offing of Cape Cod

and, in some years at least, passes westward to the offing of No Man's Land before disappearing. Thus it retraces a portion, but not all of its spring migration. The northern contingent on leaving the Gulf of Maine probably also goes by way of the offing of Cape Cod, for sometimes the latest catches are made in that locality; but more often the mackerel of this contingent disappear at the outer part of Massachusetts Bay.

The disappearance of mackerel in autumn at points north of their appearance in the springtime may be associated with a change in their vertical distribution connected with the break-down of the thermocline with autumn cooling. As has been discussed in an earlier section (p. 265), it is probable that mackerel are kept fairly near the surface of the sea in the summertime by a sharp thermocline which exists within 20 fathoms of the surface. With the cooling of the water in the autumn, surface chilling brings the temperature in the upper strata nearer to that at the thermocline, allowing greater mixture and a deepening of the upper stratum. No doubt, this is accentuated by autumn storms. Since the mackerel fishery depends on the presence of fish near the surface, this deepening of the stratum above the thermocline permits the mackerel to disappear to an ever greater extent from the range of perception of the fishermen; therefore, it is likely that in leaving the shores of their summer habitat the movement is one of descent as well as of migration southward and offshore. (See also p. 261).

EVIDENCE ON MIGRATIONS—FROM TAGGING EXPERIMENTS

The foregoing account of seasonal migrations has been based on a study of sizes of fish in the mackerel population. Tagging experiments should provide more direct evidence. Under the auspices of the North American Council on Fishery Investigations, such experiments were initiated in 1925 and were continued several years in both Canadian and United States waters. Unfortunately, they yielded disappointingly few significant returns. The bulk of recaptures was made in the same locality shortly after release and the returns from more distant localities at appreciable periods of time after releases were so few, and the evidence seemingly so conflicting, that no reasonable conclusions seemed possible.

It was particularly puzzling to find that there were a considerable number of recaptures in the United States fishery of mackerel that had been tagged in Canada, but there was only one recapture in the Canadian fishery of the mackerel that were tagged in the United States. The discrepancy was far too large to be accounted for by relative numbers of fish tagged, relative intensities of fishing or differential tagging mortality. Neither did it seem plausible that mackerel should always be going from Canada to United States waters and practically never in the contrary direction.

However, with the present knowledge gained from variations in size composition of the mackerel caught in the various localities at various times of the season the puzzling features of the tagged mackerel returns are no longer baffling and, in fact, confirm to a remarkable degree the conclusions resulting from the analysis of sizes. In examining the tagging data, their significance will be considered in relation to each of the subjects under which the migrations have already been discussed. The details of tagging methods and the records of releases and returns are given in appendix B.

Distinction Between Southern and Northern Contingents

If there are two groups, northern and southern, this should be evident from all tagging experiments, but would be revealed most strikingly by tagging during the spring mixing period off southern New England. Of the mixed population, those individuals whose sizes indicate them to be members of the northern population should provide returns showing a rapid migration northward and eastward, a minor portion reaching the western side of the Gulf of Maine and the major portion reaching Canadian waters. To be a valid test, the tagging should be done in the offing of Block Island and No Man's Land at a time when samples of the population indicate an alteration of the size composition of the sort demonstrated in the preceding pages—usually in the latter part of May. None of the tagging experiments meets this specification, but the releases of June 8 to 19 at Woods Hole (Mass.) approach it.

Although sampling was not regularly carried out in 1925, it is known from a study of the fish tagged in this experiment and from samples collected in August, September, and October of that year that the 1923-class was dominant and the 1921-class subdominant, and it is known further from the size composition in subsequent years that the 1923-

class was characteristically a southern-contingent class while the 1921-class and still older mackerel were mainly members of the northern contingent. The mackerel tagged in the experiment under consideration contained both elements roughly separable by a line drawn at 15⅜ inches, those below this length theoretically, belonging to the southern contingent, those above to the northern contingent. Thus this experiment meets the requirements of dealing with a mixed population. But it does not meet the requirement that it take place offshore along the main route of migration. Instead, the tagging was done far inshore in the bays and sounds. Hence, it might be suspected that these individuals had already split off from the main body and consist of a selected portion already committed to their area of summer sojourn. If this is true, those under 15⅜ inches belonging to the southern contingent should show a tendency to linger south of Cape Cod, indeed, might form that minor portion of the southern contingent remaining south of Cape Cod all summer. Those above 15⅜ inches, on the other hand, should pass quickly out of the southern New England area and into Massachusetts Bay either around Cape Cod or by way of the offing of southern Nova Scotia.

This expectation was confirmed by the returns from this tagging experiment (table 25). Those under 15⅜ inches were taken along various portions of the southern New England coast and even as far west as Long Island during the early months; and it was not until August that any were recaptured north or east of Cape Cod. Those above 15⅜ inches must have passed out of the southern New England area almost immediately. Aside from a few local recaptures during the first few days after release, all were recaptured east and north of Cape Cod both soon after release and during the subsequent months of the season. Hence, it is clear that the population which according to theory was identifiable from sizes as "mixed," did contain individuals which later separated according to their size into two groups corresponding in their movements as well as in their sizes to northern and southern contingents.

The returns during subsequent seasons were too few to be of much weight. Such as they are, they are confirmatory rather than otherwise, especially the one recapture in Nova Scotia in 1927. This was the only tagging experiment that was performed in United States waters that could, according to theory, provide returns from Canadian waters, and it was the only one that did provide such a return.

Migration of the Southern Contingent

According to hypothesis, mackerel tagged at any time or place in United States waters except in the area of mixing in the spring and fall, should be recaptured in United States waters.[33] This is true of all of the tagging experiments. None except the one of June 8–19, 1925, at Woods Hole, previously discussed, dealt with mixed populations and none other than this one produced Canadian returns.

Those tagged early in the spring before the time and south of the place of mixing should provide returns as far north as the Gulf of Maine. The only experiment in this category was the release May 24 to 27 of 400 mackerel in the offing of Delaware Bay. Of the two returns from this release, one was caught locally the following day, the other was taken off Cape Cod the following August. The returns, though sparse, are in accord with theory.

Those tagged during the summer in the United States waters should show random movements during the remainder of the summer and early autumn. This they did (table 26), but the random movements were perhaps fairly limited in scope, most of the individuals (254) being caught near the point of release and only a few (6) being recaptured in other areas. All recaptures were within the area forming the summer habitat of the southern contingent according to our hypothesis.

One would expect that recaptures during the late autumn of fish tagged in the Gulf of Maine would be made in the offing of Cape Cod and even west along the southern New England coast as far as Block Island. Unfortunately, only one of the mackerel tagged in the summer of 1925 was recaptured in the late autumn. This had traveled from the coast of Maine to the offing of Block Island, where it was caught October 19.

Thus, as far as they go, the tagging returns pertinent to the southern contingent are in accord with the evidence derived from size composition.

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[33] Still another exception should be made when technique of tagging marks the mackerel permanently enough to provide returns several seasons after release. Then, yearling mackerel spending the summer in the Gulf of Maine but destined to join the northern contingent as they grow older (p. 286) might be tagged in summer in the Gulf of Maine and be recaptured in Canadian waters in subsequent years. Since the tagging experiments were with impermanent tags (appendix B) this exception need not be considered.

Migration of the Northern Contingent

To be of significance in testing our theory that the northern contingent passes the southern New England coast in migrating to Canadian waters, tagging should take place in southern New England along the supposed route of migration during the period of so-called mixing in spring. From such taggings, one would expect a small portion to be recaptured in the western parts of the Gulf of Maine, but the major part should be recaptured during the ensuing summer in Canadian waters, perhaps as far north as the Gulf of St. Lawrence. Unfortunately, none of the tagging experiments took place at the time and area above specified. The experiment of June 8–19, 1925, was performed at the right time but too far inshore to be included with the representatives of the northern contingent. It apparently included mainly that segment of the northern contingent destined to spend the following summer in the Gulf of Maine (p. 301).

Failing adequate tagging experiments to test that portion of the theory involving passage of the northern contingent through United States waters on their way to Canadian waters in the spring, the next most important portion of the theory to examine is that involving their passage through United States waters on the way south in the fall. For this purpose, the reports on the releases of 7,746 mackerel in Canadian waters should be instructive. Although full results of these marking experiments have not yet been published, a preliminary account appeared in the Proceedings of the North American Council on Fishery Investigations, 1921–30 (p. 26). Also, the Biological Board of Canada (predecessor to the Fisheries Research Board of Canada) kindly furnished records on the United States recaptures of the mackerel tagged in Canadian waters. These are listed in table 19.

According to theory, all mackerel found in Canadian waters are members of the northern contingent and should pass through United States waters in spring and fall when migrating from their supposed winter habitat to their summer habitat and back again. There are two minor exceptions to this: (1) A small portion of the northern contingent, according to theory, stays in the Gulf of Maine which it enters either around Cape Cod or across Georges Bank and past Cape Sable at the southern tip of Nova Scotia; (2) another small portion, according to theory, may spend the winter at the edge of the shelf off Nova Scotia and pass directly to the coast waters in the spring and back again in the fall, without passing through United States waters.

The first of these exceptions would need to be taken into account only if the tagging took place near the southern tip of Nova Scotia in the spring, in which case, part might go westward into the Gulf of Maine and be captured there in the summertime, and part pass northeastward along the coast of Nova Scotia and would not be recaptured in waters off United States until they return in fall. The second exception would hardly be expected to influence returns to a perceptible degree, for it would tend only to reduce moderately the percentage destined to pass through United States waters. Unfortunately, the first of these exceptions affects the majority of the Canadian-tagged mackerel, for 6,812 out of the 7,746 or 88 percent were released near Yarmouth in June, at just the proper time and place to provide a high liklihood of including a considerable number of that small part of the northern contingent which is expected to enter the Gulf of Maine, passing the vicinity of Yarmouth on the way.

Looking first at the returns from the Yarmouth taggings of May and June, among the fish recaptured in the United States fishery the same season they were released, one was taken in June, one in July and three in August, all from along the coast of Maine. Hence, it appears that the Yarmouth fish did include some of that minor portion of the northern contingent that was expected to circle back into the northern part of the Gulf of Maine. Nonetheless, the major portion of Yarmouth fish must have gone eastward, as would be expected of northern contingent fish, for among the Canadian returns "over two-thirds of the fish recaptured had migrated eastward during the same summer" (North American Council on Fishery Investigations, 1932, p. 26). The context of the report from which the quotation was taken indicates that this fraction was computed on the whole first-season returns, including the fall season, and hence the fall recaptures in waters off the United States (eight in number) must have served to lower the apparent proportion of eastward migrants. Although the number of first-season returns is not given, it may be deduced. To the westward, that is, in waters off the United States, 5 were recaptured in summer and 8 in the fall—or 13 altogether. This probably

TABLE 19.—*List of mackerel tagged in Canadian waters and recaptured in waters off the United States*[1] *arranged according to month of recapture*

Tag No.	Data on release		Length in centimeters	Data on recapture	
	Date	Locality		Date	Locality
Recaptured during same season as released:					
June:					
5596	June 16, 1927	Yarmouth,[2] Nova Scotia	43	June 24, 1927	6 miles east ½ south of Halfway Rock, near Portland, Maine.
July:					
1124	June 28, 1928	do	47	July 18, 1928	Halfway Rock, near Portland, Maine.
August:					
3435	June 21, 1926	do	43	Aug. 16, 1926	Wood Island, Maine.
2832	June 9, 1928	do	48	Aug. 21, 1928	Bantam Rock, near Boothbay Harbor, Maine.
551	June 26, 1928	do	48	Aug. 22, 1928	35 miles southeast of Monhegan Island, Maine.
September:					
2142	May 30, 1928	do	47	Sept. 5, 1928	Near Scituate, Mass.
1211	June 28, 1928	do	45	do	80 miles southeast of Highland Light, Cape Cod, Mass.
7885	June 16, 1927	do	44	Sept. 6, 1927	25 miles southeast of Chatham, Mass.
1588	June 29, 1928	do	45	Sept. 9, 1928	Near Scituate, Mass.
5941	June 18, 1927	do	42	Sept. 22, 1927	4 to 5 miles southeast of Thatcher Island, Mass.
162	June 20, 1928	do	46	Sept. 24, 1928	85 miles southeast of Highland Light, Cape Cod, Mass.
October:					
1063	June 28, 1928	do	44	Oct. 10, 1928	2 miles off Cape Ann, Mass.
1282	do	do	43	do	Do.
1031	do	do	43	do	8 miles east of Thatcher Island, Mass.
1055	do	do	46	do	Do.
5731	June 17, 1927	do	40	Oct. 17, 1927	10 miles southeast of Thatcher Island, Mass.
802	June 27, 1928	do	45	Oct. 21, 1928	5 miles southeast of Rockport Harbor, Mass.
6486	Sept. 3, 1927	Flint Island, Cape Breton Island.	43	Oct. 22, 1927	10 miles southeast of Thatcher Island, Mass.
November:					
3910	June 20, 1928	Yarmouth, Nova Scotia	51	Nov. 5, 1928	15 miles northwest of Race Point, Cape Cod, Mass.
3761	June 18, 1928	do	44	Nov. 13, 1928	10 miles southeast of Thatcher Island, Mass.
December:					
6687	June 30, 1927	Dover Bay,[3] Nova Scotia	42	Dec. 23, 1927	28 miles east of Eastern Point, Gloucester, Mass.
Recaptured during season following release:					
May:					
115	June 20, 1928	Yarmouth, Nova Scotia	42	May 20, 1929	60 miles south-southeast of Atlantic City, N. J.
June:					
6075	June 30, 1927	Dover Bay, Nova Scotia	45	June 4, 1928	Lavalette, N. J.
5526	June 16, 1927	Yarmouth, Nova Scotia	42	June 17, 1928	30 miles south-southeast of No Mans Land, Mass.
507	June 26, 1928	do	47	June 18, 1929	5 miles northeast of Race Point, Cape Cod, Mass.
252	June 25, 1928	do	45	June 26, 1929	60 miles southeast of Highland Light, Cape Cod, Mass.
5643	June 16, 1927	do	44	June 28, 1928	1 mile southeast of Block Island, R. I.
July:					
6450	June 30, 1927	Dover Bay, Nova Scotia	46	July 5, 1928	Menemsha Bight, Vineyard Sound, Mass.
6353	do	do	44	July 29, 1928	8 miles southeast of Chatham, Mass.
August:					
3006	Aug. 17, 1925	Magdalen Island	40	Aug. 4, 1926	25 miles east-southeast of Graves Light, Boston, Mass.
6677	June 30, 1927	Dover Bay, Nova Scotia	46	do	50 miles south-southeast of Highland Light, Cape Cod, Mass.
6926	do	do	42	Aug. 7, 1928	Off Block Island, R. I.
October.					
732	June 27, 1928	Yarmouth, Nova Scotia	42	Oct. 11, 1929	South Channel near northern edge of Georges Bank.
372	June 25, 1928	do	45	do	South Channel.
6909	June 30, 1927	Dover Bay, Nova Scotia	42	Oct. 31, 1928	Provincetown Harbor, Mass.

[1] Available through the courtesy of the Biological Board of Canada.
[2] At Cranberry Head.
[3] At White Point.

constituted all of the westward returns and hence should be one-third of the aggregate first-season recaptures which accordingly would be 39 in number. Our interpretation is that 5 migrated westward in spring, the remainder (34) eastward, from whence they did not return until fall. Of the total, then, about one-eighth turned west after release at Yarmouth in the spring; about seven-eighths, or by far the major portion of Yarmouth spring mackerel went on their way to more easterly and northerly waters. It was the fall return of this major portion from waters off Canada that must have caused the United States recaptures of Yarmouth-tagged mackerel to rise to six each in September and October, with an additional two in November and December. Had the mackerel of this tagging experiment remained in the Gulf of Maine all summer, there should not have been such a rise in tag returns during the autumn months.

Of Canadian taggings in places other than Yarmouth, there were only two experiments, one of 108 mackerel at Magdalen Islands, and another of 826 near Canso, Nova Scotia. The returns in the summer of the season of tagging, from both these experiments, were all from Canadian waters as would be expected from theory. Those released near Canso showed "migrations to Cape Breton Island and around it into the Gulf of St. Lawrence as far as the north shore of Prince Edward Island during the same summer" (North American Council on Fishery

Investigations, 1932, p. 26). There were two fall returns in United States waters, one in October, the other in December, and both from near Cape Ann, where, according to the size-composition study, the drift-gill-net fishery exploits the schools of northern contingent mackerel on their way south through the Gulf of Maine in the fall.

A return from Sable Island Bank in January of a mackerel that had been released near Cape Canso the preceding summer confirms the possibility entertained in our hypothesis, that some of the mackerel of the northern contingent may move directly offshore and spend the winter along the edge of the continental shelf as far eastward as the Sable Island Banks. Nonetheless a return from this ground is surprising, inasmuch as there is no winter fishery for mackerel there (or elsewhere) and the chances of a tagged fish being caught incidental to other fishing seem very poor.

Returns during the seasons following that of tagging should also be instructive. Fish tagged in Canadian waters should be recaptured in waters off the United States the second and subsequent years, mainly in the spring and fall, very few in the summer. The 14 second-season recaptures took place as follows: One in May, five in June, two in July, three in August, and three in October. Thus the spring (June) returns had the expected superiority in numbers, but the summer returns were higher, and the fall returns lower, than expected from evidence on migrations of the northern contingent gained from the size-composition studies. This might be taken as evidence that mackerel which are members of the northern contingent in 1 year may forsake that contingent in others but there is another explanation for these tagging results which appears preferable.

This alternative explanation involves consideration of the effect of the tagging on the mackerel itself. Several tagged fish of the second-year returns came into our hands for inspection, and the condition of others where only the tag was returned was ascertained by correspondence with the parties capturing the fish. In all instances in which pertinent information could be obtained, the caudal peduncle, around which the tag was carried, was chafed, sometimes rather severely, and about half of the fish were emaciated. Thus, at least a portion of the tagged fish must have been severely weakened by the second season and might have been expected to lag behind the more vigorous untagged population with which they were to migrate. Corresponding with this expectation, mackerel marked with tags Nos. 115, 6075, 6450, 6926 were taken from southerly localities well after the time the main populations of both southern contingents and northern contingents had passed by, and Nos. 6353, 3006, and 6926 were taken from localities well after the northern contingent had passed by, though the southern contingent had not done so. Thus it appears likely that such of the tagged fish of the northern contingent as "joined" the southern contingent a year following, did so by lagging behind their companions because they were weakened by the tags.

That this did not represent a general joining of the southern contingent by members of the northern contingent is suggested by the fact that only 7 of the 14 second-season recaptures in waters off the United States of Canadian-tagged mackerel need be classified as "laggards." The others were taken at times and places appropriate for the northern contingent to have been passing through waters off the United States. Presumably still others of the same tagging lots passed through these waters without being recaptured and reached Canadian waters where, if caught, they would constitute second-season Canadian recaptures of which I do not have the records. It is possible that the so-called laggards may constitute a relatively small proportion of the tagged groups and their lagging in any case may not represent an event commonly encountered in normal uninjured mackerel.

Summary of Tagging Evidence

Tagging experiments, though not designed properly for the purpose, and therefore inadequate in many respects, substantially corroborate the evidence obtained from the size composition as to (1) existence of the two contingents, northern and southern, (2) the migration of the southern contingent from the offing of Virginia to the Gulf of Maine but not farther, (3) their departure from the Gulf of Maine around Cape Cod in the fall, (4) the migration of a portion of the northern contingent from southern New England into the Gulf of Maine, (5) the migration of this contingent northwesterly from southern Nova Scotia into the Gulf of St. Lawrence, (6) their return through the Gulf of Maine in the fall, and (7) the repetition in part of this migration in the year following tagging. The weakest link in the tagging evidence is its failure to demonstrate the migration of one portion of the mixed population

directly to Canadian waters while the other part remains in United States waters. This is due to lack of tagging in offshore waters of southern New England at the time the two contingents mix. Tagging experiments designed to examine this point are to be desired. In performing such experiments the experimental information of suitability of different styles of tags (appendix B, p. 356) should be useful.

MIGRATION OF YOUNG MACKEREL

JUVENILE MACKEREL

During the first month or two after hatching, mackerel drift in the upper layers of the sea as more or less helpless members of the plankton community. Toward the end of July in American waters, they attain a length of 50 millimeters (2 inches), are active swimmers, and aggregate in schools (Sette 1943: 177–178). Young mackerel as small as 5 to 10 centimeters (2 to 4 inches) long were collected only in inshore locations. Small schools of such mackerel wander into pound nets along shore where the water is only several fathoms deep, and on a few occasions when it was possible to visit the pound nets before they were hauled, series of such mackerel were collected with a dip net. The main spawning grounds are well offshore, and earlier plankton catches of mackerel larvae have always been offshore, also. So these young mackerel taken alongshore in late July and early August must have migrated some tens of miles toward shore and probably some distance alongshore as well. Whether the entire population of young mackerel at these sizes is involved in such an inshore migration is not known. No fishing gear is operated for the purpose of catching these sizes either inshore or offshore, and the presence of vast numbers in either zone might easily remain undetected.

By September, these mackerel become large enough to be retained, along with other fishes, in the commercial pound nets when they are hauled. They are about 8 inches long, known as tacks and spikes, and considerable quantities are caught during the fall months of the year, mainly along the coast of southern New England and along the shores of the Gulf of Maine as far north as Casco Bay.

Although practically all of the catches are by shore gear such as pound nets, traps, and weirs, it is not necessarily true that the entire population has migrated to the shore line, because occasionally a few tack- or spike-sized mackerel are found hanging in the meshes by their teeth when gill nets are hauled in offshore waters. Also, late in fall, the spike-sized mackerel sometimes plug the meshes of offshore purse seines. They have been known to fill the meshes so extensively that the purse seine cannot be handled safely and instances of loss of such plugged seines have occurred. For this reason purse-seiners exercise extreme caution not to set the seine around schools of mackerel of this size. Thus, although offshore catch records are rare, it is quite possible that a large part of the population may remain offshore in addition to the ones known, from the pound-net catches, to have migrated inshore.

From studies of size composition of samples of juvenile mackerel taken by the pound nets alongshore it appears that there are local subpopulations in many localities. That is, the samples from a given locality tend to be uniform through successive weeks, except for progression to larger sizes with growth, and tend also to differ markedly from the size composition of samples taken simultaneously in other localities.

Although the predominant tendency is toward uniformity within a locality and differences between localities, there are exceptions, when the size compositions appears to differ erratically in successive samples at a given locality. Such irregularity is more common where points of land jut out into the ocean, as at Montauk and Provincetown, than in large coastal indentations as Buzzards Bay and Vineyard Sound. It is also more common toward late fall in all localities.

This evidence in its entirety suggests that the juvenile mackerel tend to aggregate into relatively stable subpopulational units which remain more or less intact during summer and fall. Some of the units remain fairly localized, others roam more widely. But the mixing between units, if any, is too slight to bring about homogeneity in size composition along the American coast.

With the approach of winter the movements of the various aggregates apparently become more pronounced and probably successions of them pass through a given locality in making their fall departure from coastal waters. The latter may be at least as late as November in some years, for samples of the juvenile mackerel have been taken up to the end of November. Whether any remain until still later would not be known from our sources of

information because the pound nets usually are dismantled at this time in anticipation of the hazards of winter storms.

It is not known whether or not there is a broad division of the juvenile mackerel into northern and southern contingents, such as exists among the adults. Samples of juveniles were not taken from Canadian waters during this investigation, and I have not found published records concerning them. Presumably, the considerable spawnings in the Gulf of St. Lawrence give rise to juveniles which should be found around the shores of the Gulf and even along the outer Nova Scotian coast in the late fall. These, conceivably, might pass through coastal United States waters on their way to their wintering grounds. I can see no clear-cut evidence of this among our samples. Possibly the greater irregularities of size composition in the late fall are partly due to the passage of Canadian-reared juveniles through United States waters, but from the existing evidence it seems more probable that these are but expressions of the movements of the previously more localized aggregates within United States waters.

YEARLING MACKEREL

In their second year of life mackerel range from about 25 centimeters (10 inches) long in early summer to about 32 centimeters (13 inches) long by fall and are usually termed "blinks" or "tinkers" by fishermen and by the fish trade. They are in commercial demand, though usually commanding a lower price than adult mackerel. Samples are available from both pound-net and purse-seine catches. They seem not to be caught regularly by drift-gill-netters, no doubt, because the meshes of the nets are too large to gill them.

Though occasional samples of tinker mackerel have been found among the spring catches by both purse seines and pound nets, important quantities were never taken by purse seines until July or August during the 10 years of this investigation. Pound nets have yielded samples of tinkers somewhat earlier, in May of some years, but more often in June. This is in contrast with adult mackerel which were often caught by purse seiners in large quantities in the first half of April and always in the last half.

Assuming that the absence of catches of tinker mackerel is evidence of their absence from the fishing area, it would seem that the tinker mackerel were about a month later than the adults in arriving along the shore waters where the pound nets are located and several months later on the offshore purse-seining grounds. The assumption perhaps is justified for pound nets but not necessarily true for purse seines because with the latter method of fishing, the aggregation into schools and the vertical distribution of the schools in the water would determine whether or not they could be caught and, furthermore, with adult and tinker mackerel schools equally available the purse-seiner probably would seek the former rather than the latter on account of the price differential. Taking the various elements of evidence into account and recognizing their respective limitations, one may conclude only that the tinker mackerel normally do not migrate in company with the adult mackerel in the spring migration, and though their routes may be similar the tinkers are substantially later in arriving. It is probable that during late spring and early summer some of them at least tend to be close to shore, for they "run" into pound nets. Whether some are also offshore is in doubt. If present in offshore waters, they either are too far below surface or they are in schools too small to be economically attractive to purse seiners. The latter appears to me more probable for I have seen tinker mackerel in and near the western end of Vineyard Sound which were distributed in countless small schools each containing several scores to several hundreds of individuals. The fishermen call such aggregates "pods" and never try to net them.

As summer progresses, the tinker mackerel obviously aggregate into larger schools, for in July of some years and in August of others the purse seiners begin to catch them in large quantities and usually continue to do so until the end of October. Their summer catches of tinker mackerel have a range along the coast line identical to that of the adults, but average substantially closer to shore. Massachusetts Bay, Ipswich Bay, and the waters along the eastern face of Cape Cod perhaps furnish the bulk of tinker mackerel catches by purse seiners.

Like the juveniles, the yearlings tend to remain somewhat localized, once they have reached their summer habitat. This is evidenced by the great predominance of local as compared with distant returns from a few tagging experiments (see appendix B) and also from the comparatively uniform size composition among successive samples from the same area coupled with the differences in size composition of samples taken simultaneously from

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different areas. However, the localization, as far as it may be detected from size composition, is not so severe as among the juveniles. In general, there are fairly consistent differences in size composition as between the areas north of Cape Cod and those east and south. Within these two broad regions, the differences are much less pronounced and much less consistent.

Minute examination of this subject through size composition is complicated by the fairly rapid growth of yearling mackerel which changes the size composition sufficiently in successive short periods of time to preclude statistical tests based on simple assumptions and a full report on this subject must await future study of the growth of yearlings.

In all of the years of this investigation, purse seining either stopped or had negligible success after the end of October. With the end of purse seining, samples of young mackerel also cease to be available. It may be presumed from this that the yearling mackerel depart from United States waters along with adults of the southern contingent. Whether or not they are replaced by yearlings from Canadian waters which would be comparable to the northern contingent as recognized among adults cannot be known from our data because the only fishery taking place in waters off the United States at an appropriately late period of the year is by drift-gill-nets, the meshes of which are too large to sample the range of yearling sizes.

In summary, it has not been established that there are northern and southern contingents among the young mackerel. The migrations of the latter parallel those of the southern contingent as it is known among adults. This would be interpreted to mean that there are two contingents among the young and that only the southern one came within the observational scope of this investigation, or, alternatively, it could be interpreted to mean that all of the young behave as a single population with a migration pattern like that of the southern contingent, and that it is only in later adulthood that mackerel segregate into two contingents.

To discover which alternative is correct would require investigations on young mackerel in Canadian waters parallel with similar investigations in United States waters. The problem, I believe, would be solvable both by the tagging method, employing the internal type tag, and by the study of size composition. Its solution would have vital bearing on the fundamental question of whether or not the northern and southern contingents, as recognized among adults, are genetically discrete population entities. The conclusions reached would be critical in determining administrative policy in the development and maintenance of this mackerel resource. This field is perhaps the most important and promising for further advancement of knowledge regarding the mackerel population.

MORPHOMETRIC EVIDENCE

During the course of investigations, and before the existence of the two contingents was suspected, a brief survey was made of the possibilities of detecting subpopulations by differences in form and meristic characters. Various body proportions and counts of spines, rays, and finlets were recorded for a number of samples from several localities.

It was soon evident that a number of difficulties would be involved in such studies. The anterior spines of the first dorsal become covered with the integument in large individuals, the last ray of the second dorsal and of the anal is sometimes partially divided, and the body proportions change with size of the individual. To detect slight differences in any count or measurement, it is necessary for some characters to make time-consuming examination and for others to discount the influence of size of individual by rigorous statistical methods. Since the greatest interest would be attached to differences between the mackerel from waters off Canada and those from off the United States, and since the ranges in sizes available from these two regions did not overlap extensively in the season of survey of this subject, the discounting of size influence by comparing identical sizes or by studying the regression of a character on length was not then feasible. There were indications that some of the characters examined might be significantly different, but conclusive evidence obviously would require large scale activity. Therefore, the brief survey was terminated pending the opportunity of embarking on a comprehensive project in this field.

With the information now available from the study of size composition and from tagging, it would be possible to intelligently concentrate a morphometric study on certain time-place groups of samples that would be critical either for tests of the conclusions reached by other methods or for supplementing the present information in certain important respects. By so concentrating the effort, this method could be employed much more efficiently than would have

been possible at the time of the initial survey of its feasibility. Even so, the more important questions to be examined would require extensive material extending through a number of seasons.

Thus, to investigate the nature of the two contingents one would need to examine samples of a year class as it passed through a number of years of life. By assembling morphometric data on parallel series of samples from Canadian and from United States waters through the juvenile and yearling years, and for the successive later years of life, adding a third series consisting of samples from the northern contingent taken as it passes through United States waters on its northward journey in the spring and on its southward journey in the fall, one might expect facts to emerge that would be significant to the elucidation of the nature of the two contingents, and the contributions of each to the mackerel yield of both the United States and Canadian fisheries.

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APPENDIX A.—LENGTH-FREQUENCY RECORDS

Most of the evidence upon which the conclusions of this paper rest consist of the results of tagging experiments and of the length composition of the mackerel stock as it is known from the measurement of samples from the commercial catch. The tagging results are recorded in appendix B. In this appendix will be given the basic records of size composition.

COMMERCIAL CATCH

From the statistics of 1927 to 1930 it may be estimated that the offshore fleet accounts for approximately 70 percent of the total catch and that miscellaneous alongshore fisheries, mainly inshore small-boat gill nets, pound nets, and traps, account for the remainder (Sette and Needler 1934: 16 and 23). Of the offshore fleet's catch, about 90 percent is taken by purse seiners and 10 percent by drift-gill-netters (Sette and Needler 1934: 23).

Purse-seine vessels, known as "seiners," are relatively large, averaging in 1929 about 35 net tons (register measure), and they carry crews of about 12 men, while the drift-gill-netters, known as "netters," are smaller, averaging below 20 net tons, and carry about 7 men. As might be expected, the seiner catches normally are larger than the netters' catches. Seiners fish throughout the "mackerel season" while netters typically fish only in spring and fall.

During this investigation Gloucester was the home port for most of the vessels of both fleets, with a few fishing out of Boston. Although based on Gloucester, the fleet delivered most of its catch to other ports. In a typical season about one-third of the seiner fleet sailed early in April to engage in the "southern" fishery off the Virginia capes, landing their early catches at Cape May, Wildwood, and sometimes Atlantic City, N. J. By May nearly the entire fleet was out and the fishing was off the New Jersey-Long Island coast, with most of the catch landed at New York. Toward the end of May the fishing area was mainly off the southern New England coast with some of the catch going to New York and some to Boston. At this time a portion of the fleet customarily sailed for the Nova Scotian coast ("Cape Shore"). These vessels brought their fares back to Boston and rarely made more than one Cape Shore trip. By mid-June the entire fleet was usually fishing in the Gulf of Maine and landing the fish at Boston and Gloucester. Boston usually received mackerel most regularly, with fares going to Gloucester for salting and canning mainly when the fresh-fish market and freezers were glutted with mackerel.

SAMPLING THE CATCH

With one man regularly available to sample the catch, it was possible to cover the entire range of the vessel fishery by starting at Cape May in April, shifting to New York as soon as landings were substantial there and, finally, to Boston as soon as a substantial portion of the landings were made there. Since it was not always possible to anticipate the shift of landings from one port to another, sometimes there was a gap of several days in the sampling series. On the other hand, it was possible sometimes to have samples taken at several ports simultaneously when extra employees were available.

Sampling was done daily, and samples were drawn from as many fares as time permitted. Often samples were taken from every fare arriving at the port, though when landings were numerous this was not possible. On the average, samples were taken from about 800 seiner catches and from about 200 netter catches each season. This was equivalent to about 28 percent of the total number of seiner catches and about 24 percent of the total number of netter catches per season.

In taking a sample, first the skipper or a responsible crew member of the vessel was questioned as to the date, time, and locality of catch, and the number of sets made. Then, as the mackerel were unloaded, a number of mackerel, taken at random, were measured. The standard number for a sample was 20 fish, but when opportunity afforded and special purposes were in view, 40, 50, or 100 fish were measured.

In addition to his sampling of the vessel fishery, the regular sampler was often able to take measurements of trap-caught mackerel from known sources shipped overland to the principal ports; also, at Woods Hole, Mass., Montauk, N. Y., and occasionally other alongshore localities, trap and pound-net mackerel were measured by personnel primarily engaged in other duties. The coverage of this

pound-net and trap fishery was far less thorough and less consistent than the vessel fishery. It varied from 8 samples containing 300 fish in the season of minimum sampling to 250 samples containing 13,000 fish in the season of maximum sampling during the 10 years included in this investigation.

MEASURING THE FISH

Measurements were taken on a measuring board having a nose block at one end and a measuring scale inlaid along the middle of the board. Since it was often necessary to employ the measuring board in places where it could not be set on a horizontal surface, additional beveled blocks were set along the longitudinal margins of the board to form a trough that not only prevented the fish from sliding off the board but also gave some assurance that the fish was correctly positioned on the board. In measuring, the fish was laid on the board, after flexing when rigor mortis was present, so that the snout was lightly pressed against the nose piece and the longitudinal axis of the body lay along the graduated scale. The latter was graduated in half-centimeters and offset one-quarter centimeter from the nose block. By reading to the first graduation mark unobscured by the tail, a measurement was obtained which gives the straight-line distance from tip of the snout to the tip of rays at the middle of the fork of the tail to the nearest half centimeter. The length therefore corresponds to the measurement which Ricker and Merriman (1945: 185) have named "median length" and for which they recognize also the alternative designations of midcaudal length or fork length.

To avoid personal bias in favor of whole or half-centimeter marks, the measuring scale had uniform graduation marks and they were serially numbered. In addition to avoiding bias, this had the advantage of giving two-digit numbers for all listings and computations, the data being divided by two for conversion to centimeters only at the final stage of work.

SUMMARIZING THE DATA

Data on the locality of catch were received from the fishermen in terms of distance and bearing from headlands. For purposes of portraying the distribution of catches, they were plotted on mercator projection charts and summarized by 10-minute rectangles of latitude and longitude. But such fine divisions were not practical for summarizing the length-frequency records, so the much coarser pattern of statistical areas adopted by the North American Council on Fishery Investigations was used to classify the samples by catching locality. This system designates the larger regions by Roman numerals and their subdivisions by capital letters. Since the North American Council had not subdivided its area XXIII, we have divided it into subareas for the purposes of this investigation. The North American Council statistical areas and subareas as they existed at the time of this investigation, and our own subareas for area XXIII are shown in figure 1 for mackerel fishing waters. Some of the North American Council's subarea boundaries have since been revised but not in places materially affecting the locality designations used in this report.

For purposes of summarizing the records by periods of time, two basic units were used: 5-day periods and half-month periods. In 31-day months the final "5-day" period of a month actually contained the 6 days running from the 26th to the 31st, inclusive, and the final half-month contained 16 days running from the 16th to the 31st, inclusive. In 1933 and 1934 the purse-seine fleet operated under a system of limitations intended to curtail the landings. This system affected the activities of the fleet by time units of calendar weeks, and for these two seasons our data were summarized by calendar week and calendar biweekly units of time.

DATA INCLUDED

In the present study of migrations by the method of size-composition comparisons, use is made of the length-frequency distribution in geographical units of statistical subareas and in time units of 5-day periods (weekly periods in 1933 and 1934). The tables in this appendix are intended to give the source data and should be in the same units. However, to save space, the data have been combined by 10-day periods in certain instances where the frequency curves were similar in successive 5-day periods. Furthermore, to conserve space it has been necessary to omit certain entire categories of data. These were selected so as to minimize the loss of evidence significant to migrations. Omitted are:

1. All samples from pound-net and trap catches. These were taken intermittently, at only a few points along the coast and are not adapted to systematic portrayal of size-composition changes in time and space. Insofar as comparable place and time records are available, the size composition of mackerel catches of traps and pound nets in spring is

similar to that of the purse-seine catches in spring. In summer, however, the pound nets and trap catches lack the adult sizes of mackerel.

2. All samples from spring and summer drift-gill-net catches. These differ from the purse-seine catches slightly. Because the differences may be due to mesh selection, it is doubtful whether or not they represent a true difference in the population sampled by this fishery.

3. All samples of yearling and younger mackerel, where occurring unmixed with adult mackerel, in summer and autumn catches. These are to be presented in detail in a report to be prepared on the subject of growth rates.

4. All samples from the summer purse-seine fishery; however, a summary table of length-frequences for the summer-fishery samples as a whole is given in table 24.

5. All samples prior to May 1 of each year. The mackerel catches prior to May 1 were so nearly identical in size composition with those from the first half of May that the latter serve to give the early-spring composition.

The remaining data cover the seasons, spring and fall, when evidence of migrations is given by changes in size composition. Table 20 gives a list, by date and statistical subareas, of number of fish measured; and table 21 gives the length frequencies of these measurements, by date groups and statistical subareas, for May and June of each year. The corresponding data for the fall fishery are given in tables 22 and 23. For the year 1933 a discrepancy will be noted between the numbers of fish listed in tables 22 and 23. This is due to the omission from table 23 of mackerel under 32 centimeters.

TABLE 20.—*Numbers of mackerel from purse-seine catches measured in May and June from statistical areas XXII and XXIII, by date and statistical subarea*

1926 [1]

Date	Area XXIII				Area XXII											
	C	B	B [2]	A	R	R [2]	Q	Q [2]	P	P [2]	O	G	G [2]	E	E [2]	D [2]
May 3	40															
May 4	160															
May 5	140															
May 6	80															
May 7	[3] 320	40														
May 8	[3] 180	100														
May 10	[3] 40	280														
May 11		280														
May 12		300														
May 13		40														
May 15				60												
May 17		20	200	60												
May 18		60	80													
May 19		20	80	20												
May 20			240													
May 21			120													
May 22		20	80													
May 24			180													
May 25			40													
May 28						60				20						
May 29						40										
June 1						20		120		100					80	
June 2															40	
June 3															100	
June 4															140	
June 5															79	
June 7															120	
June 8															20	
June 9															140	
June 10														80	80	
June 11										40				200	80	80
June 12						40								20	80	
June 14		20					60				20				200	20
June 15										20						40
June 16							80									
June 17							40				40				40	
June 18							120		40							
June 19					40		140		20							
June 21					80				20		100					
June 22							120		20		100				20	
June 24					40							40				
June 25					200										40	
June 26												80				
June 28												300	20		60	
June 29												240	20			
June 30					20							40			20	

[1] In addition to the numbers listed in the table for 1926, there were 620 mackerel measured from drift-gill-net catches in area XXIII during the period from May 1 to 15 that were unclassified as to date and subarea and 20 each from purse-seine catches on May 7, 8, and 10 that were unclassified as to subarea.

[2] From drift-gill-net catches.

[3] Includes 20 fish not classified by statistical subarea.

TABLE 20.—*Numbers of mackerel from purse-seine catches measured in May and June from statistical areas XXII and XXIII, by date and statistical subarea*—Continued

1927

Date	Area XXIII				Area XXII				
	D	C	B	A	S	R	Q	P	O
May 1	160	60							
May 2	140	460							
May 3	20	140							
May 4		240	100						
May 5		60	20						
May 6		140	260						
May 7		54	99						
May 9		20	376	26					
May 10			[4] 139						
May 11			100						
May 12			60						
May 13			60						
May 14			20						
May 17							40		
May 20					100		100		
May 21				40	80		[5] 200		
May 22							120	20	
May 23					80		250	20	20
May 24							80		
May 25					20		60		
May 26							60		
May 27							140		
May 28							250		
May 31							160	20	40

Date	Area XXIII				Area XXII				
	D	C	B	A	S	R	Q	P	O
June 1						20	100	20	40
June 2						20	420		20
June 3							220		40
June 4							300		20
June 5							20		
June 6							180		
June 7							120		
June 8							160		80
June 9				20	20		200	40	120
June 10					60		160		60
June 11					100		240		40
June 12							20		
June 13				120		20	280		160
June 14					140		200		100
June 15							100		440
June 18							40	100	360
June 22							80		
June 23						60	60		[6] 20
June 24						40	160		
June 25					60	20	[5] 180		
June 27					40		200		
June 28					40		[7] 160	40	
June 29							180	20	[6] 20
June 30					60		180	20	

[4] Includes 39 not classified by subarea.
[5] Includes 20 not classified by subarea.
[6] From XXII D.
[7] Includes 40 not classified by subarea.

1928

Date	Area XXIII			Area XXII			
	C	B	A	R	Q	P	O
May 7	20	20					
May 8		140					
May 10		40					
May 11		80					
May 14		238	20				
May 15		240					
May 16		160	40				
May 17		296	100				
May 18		240	180				
May 19		180	20				
May 21		100	80				
May 22		20	140				
May 23			120				
May 24		20	186		20		
May 25			140		20		
May 26				40	80		
May 28				120	60		
May 29				109			
May 31				20	100	60	
June 1					140		

Date	Area XXIII			Area XXII			
	C	B	A	R	Q	P	O
June 2					60	20	
June 5					120		
June 6					100	60	
June 9					200	60	
June 11					160	40	
June 12					260	40	
June 13				20	140	60	
June 14					143		
June 15					80	100	
June 16					100	100	
June 18					240	100	20
June 19					260	20	20
June 20					60	20	
June 21					180	40	
June 25					260	40	80
June 26					180	40	
June 27					80	40	
June 28					120	40	
June 29					80	160	40
June 30					140	60	20

TABLE 20.—*Numbers of mackerel from purse-seine catches measured in May and June from statistical areas XXII and XXIII, by date and statistical subarea*—Continued

1929

Date	Area XXIII			Area XXII					Date	Area XXIII			Area XXII				
	C	B	A	Q	O	H	G	E		C	B	A	Q	O	H	G	E
May 1	320								June 10				233				
May 2	353								June 11				40				
May 3	75								June 12				201				40
May 4	[8] 30								June 13				80				20
May 6		206	20						June 14				153				
May 7	60	90							June 15				174				[9] 64
May 8		72							June 17				95				95
May 9		180	20						June 18				[10] 227	60			
May 10		140	140						June 19				113	60			20
May 11		80	40						June 20					104	25		20
May 13		20	100						June 21					108	20	45	
May 15			20						June 22					40		120	
May 24			175						June 24					40	40	63	136
May 25			71						June 25					40	20	126	90
May 27			65						June 26							[11] 175	
June 4				104					June 27							95	126
June 5				260					June 28							196	40
June 6				343	40				June 29							[12] 225	
June 7				92	40												

[8] From subarea XXIII D.
[9] Includes 32 from XXII D.
[10] Includes 167 from XXII R.
[11] Includes some fish from adjacent portion of subarea O.
[12] Includes some fish from adjacent portion of subarea H.

1930

Date	Area XXIII			Area XXII						Date	Area XXIII			Area XXII					
	C	B	A	R	Q	O	H	G	E		C	B	A	R	Q	O	H	G	E
May 1	[13] 398									June 5					252				
May 2	40									June 6				20	264				
May 3	36									June 7					134				
May 5	20									June 9				36	248				
May 6	20									June 10					[13] 172				
May 7	52									June 12					257				
May 9		96								June 13					220				
May 10		36								June 14					40				
May 12			25							June 17					180				
May 19			22		[14] 40					June 18					285				
May 20			124	25	91					June 19					100				
May 21					60					June 20				20	40				135
May 22					80					June 21					184				
May 23					65					June 23					100	135	102		70
May 24					25					June 24					50	[15] 140		60	20
May 26					20					June 25						30		175	
May 29					50					June 26						[16] 76		137	20
June 2					263					June 27						[16] 20	45	186	
June 3					76					June 28						20	45	40	20
June 4					140					June 30						36	120	60	

[13] Includes 25 from XXIII D.
[14] Includes 20 from XXIII S.
[15] Includes 32 from XXIII S.
[16] Includes 20 from XXIII P.

TABLE 20.—*Numbers of mackerel from purse-seine catches measured in May and June from statistical areas XXII and XXIII, by date and statistical subarea*—Continued

1931

Date	Area XXIII				Area XXII			
	D	C	B	A	S	Q	O	H
May 1	100							
May 2	310							
May 4	220							
May 5	80							
May 6	120							
May 7	[17] 190	20	50					
May 8	190							
May 9	[17] 20	40						
May 11			100	40				
May 12			120	20				
May 13			140					
May 14			100	20				
May 15				147				
May 16				123				
May 17				54		37		
May 18				60				
May 19						72		
May 20				101				
May 21				43				
May 22					80			
May 23				80	22	52		
May 27						95		
May 28						57		
May 29						75		
May 31						72		
June 1						80	40	
June 2						208		
June 3					120	200		
June 4					65	80		
June 5					40	40		
June 6						276		
June 8						60		
June 13						100		
June 15						389		
June 16						15		
June 17					40	80		
June 18					[18] 30	210		
June 19						200		
June 20					[18] 20	220		
June 22					[18] 40	200		
June 23						80		
June 24						200		
June 25						140		
June 26						120		70
June 27						80	[19] 60	[20] 120
June 29								40
June 30						60	20	20

[17] Includes 20 not classified by subarea.
[18] From XXII R.
[19] Includes 20 from XXII P.
[20] Includes 60 from XXII G.

1932

Date	Area XXIII				Area XXII				
	D	C	B	A	S	Q	O	G	E
May 1	74								
May 2	80	75							
May 3		185							
May 4		177	124						
May 5		561	25						
May 6			100						
May 7		80	20						
May 9		20	330	20					
May 10			40	60					
May 12				20					
May 15				20					
May 16				155					
May 17				40					
May 18						50			
May 19				25					
May 20						[21] 40			
May 22						48			
May 24						99			
May 25							109		
May 26						73			
May 28						25			
May 29						50			
May 30						75			
May 31						180	25		
June 1							85		
June 2							235		
June 3						80	450		
June 4						30	220		
June 5					25				
June 6					140	85	90		
June 7					215	105			
June 8					75	40	30		
June 9							200		
June 11							100		
June 13							40		
June 14							320		[22] 40
June 18							140		
June 21							[23] 320		
June 22							290	[24] 20	
June 24								20	
June 27									20
June 28								20	20
June 29									180
June 30									40

[21] Includes 20 from XXII R.
[22] From XXII F.
[23] Includes 50 from XXII P.
[24] From XXII H.

TABLE 20.—*Numbers of mackerel from purse-seine catches measured in May and June from statistical areas XXII and XXIII, by date and statistical subarea*—Continued

1933

Date	Area XXIII			Area XXII				Date	Area XXIII			Area XXII			
	D	C	B	Q	O	G	E		D	C	B	Q	O	G	E
May 1		160						June 7					100		30
May 2	40	85						June 10					100		
May 3	80	80						June 14				50	170		
May 4		140						June 15				60	180		20
May 5		130						June 16				20	100		60
May 6			25					June 19					40		80
May 8			76					June 20				170	60		
May 10			25					June 21					90		70
May 15			110					June 22				60			
May 18				110				June 23							20
May 22				110				June 24					20		
May 31				40				June 26					20		120
June 1				225				June 27						30	190
June 3				50	100			June 28					50	90	80
June 5				60	383			June 29					80		30
June 6					170			June 30							40

1934

Date	Area XXIII			Area XXII					Date	Area XXIII			Area XXII				
	C	B	A	S	Q	O	G	E		C	B	A	S	Q	O	G	E
May 3	[25] 590	100							June 6					[28] 1175			
May 7	731	390	100						June 12								140
May 8	200	20							June 13					150	120		
May 9	50	600							June 14						100		
May 10		512							June 15					320			
May 11		94							June 16					80	100	40	
May 12			100						June 18					220			50
May 14		150	330						June 19					252			120
May 15		80	360						June 20					80			
May 17		100	50		150				June 21					60			
May 18				31	381				June 22					160			
May 19				[26] 80	150				June 23					100			
May 22					250				June 25					160		100	
May 23					100	101			June 26					200		120	
May 24					110	100			June 27					280		90	
May 25					350	60			June 28					80			40
May 26					300	20			June 29					40			
May 29					[27] 1370	80											

[25] Includes some from May 2 and 4.
[26] From XXII R.
[27] Includes all samples from May 28 to June 2.
[28] Includes all samples from June 4 to 9.

1935

Date	Area XXIII		Area XXII				Date	Area XXIII		Area XXII			
	B	A	S	Q	H	E		B	A	S	Q	H	E
May 1	40						May 31				151		
May 2	590						June 1				302		
May 3	539						June 3				303		
May 4	300						June 4				250		
May 6	460						June 5				154		
May 7	540						June 6				302		
May 8	490						June 7				252		
May 9	330						June 8				99		
May 10	240						June 10				351		
May 11	160						June 11				50		
May 13	200						June 12				200		
May 14		190					June 13				200		
May 20				50			June 17				350		
May 22				400			June 18				403		
May 23			100	101			June 19				202		
May 24				90			June 21						203
May 25			101	99			June 22				51	76	102
May 27	50		50	450			June 24			[29] 51			304
May 28				400			June 25					[30] 50	303
May 29				51			June 26						962

[29] From XXII R.
[30] From XXII G.

TABLE 21.—*Length frequency of mackerel in May and June 1926 to 1935, inclusive, by time periods and by statistical subareas*

[All are from catches by purse seines except those noted for 1926 which are by drift gill nets. For region number see table 19]

Length, centimeters	May 1926					June 1926												
	1–15	16–20	21–25	26–30		1–5				6–10	11–15				16–20	21–25	26–30	
	(1)	B	B	P	R	E	P	Q	R	E	D	E	P	R	E	E	E	G
29.0	1																	
34.5																	1	
35.0		1															1	
35.5	4		3									1						
36.0	12	4	5					3	1								4	
36.5	35	16	11			1		7		3		1					5	1
37.0	38	39	34			1		5	1	6	4	7				4	2	2
37.5	94	72	46		1	3		6	1	10	2	11		1	2	4	8	6
38.0	119	106	68		1	9	3	16		13	5	12		1	2	9	15	6
38.5	97	93	56	1	2	14	4	14	2	12	4	19	2		4	10	15	7
39.0	77	79	47		4	15	5	6	1	17	4	22	2		4	6	6	7
39.5	38	44	33	2		23	5	4	1	20	9	29	3	1		3	5	3
40.0	24	26	7	1	1	47	2	6	1	26	11	28			5	7	5	1
40.5	22	7	10		3	49	3	1	1	36	19	45	1	1	1	3	3	4
41.0	4	4	7	1	4	50	4	7	2	28	14	47		4	3	2	3	1
41.5	6	5	3	2	3	37	2	1		40	17	34	1	1	5	4	1	
42.0	5	2	3		2	38				26	11	27		2	1		3	
42.5	1	4	2	1	3	16	1	1		24	7	13	1		2	1		1
43.0	2	6	5			7	2	1		13	5	9	1	1	2			
43.5	1	6	6	2	3	8				7	1	6	2		1			
44.0	11	4	7	1	4	10	2	3		3	3	9	3		2		1	
44.5	1	7	5		5	12	3	2	2	12	2	7	1	1		1		
45.0	7	10	5		6	10	10	6		13	5	9	4	2	2	1		1
45.5	2	19	9	3	10	21	9	6	1	10	5	6	2	3	2	1		
46.0	10	10	15	1	10	15	8	4	2	12	4	5	8	4		1		
46.5	6	9	10		15	18	7	7	2	10	4	6	9	6	1			
47.0	2	8	8	2	5	9	12	4		10		5	8	4		3		
47.5		3	8	2	8	8	2	2		5	1		4	2				
48.0		9	6		4	9	7	4		1	3	1	2	5				
48.5	1	5	1		1	2	6	1		2			2					
49.0		1			1	7	3	1	1	1			3	1			2	
49.5				1	1			1	1									
50.0					2										1			
50.5								1				1	1					
51.5		1			1													
Total	620	600	420	20	100	439	100	120	20	360	140	360	60	40	40	60	80	40

Length, centimeters	May 1926					June 1926											
	1–10		11–20		20–31	1–10	11–15				16–20				21–30		
	B	C[2]	A	B	B	E	B	E	O	Q	O	P	Q	R	G[3]	O[3]	R[4]
33.0																	5
33.5													3		1		3
34.0													3	1	2		4
34.5	1												2	2	4		6
35.0		1		1											6		16
35.5	2	11	3	7									6	1	2	1	13
36.0	9	39	5	26	1	1		2			3	1	21	1	10	4	22
36.5	33	97	13	48	1	1		3	1	4	1	8	46	2	18	6	34
37.0	69	160	24	111	5	4		6	3	7	3	9	58	7	53	27	72
37.5	85	198	27	148	3	6		12	3	7	8	24	81	5	135	36	78
38.0	97	178	11	130	5	5	2	19	3	6	7	7	87	7	156	36	71
38.5	56	139	16	103	3	4		21	3	7	7	8	29	4	125	32	58
39.0	26	53	10	57	1	6	2	13		4	1	2	16	5	93	16	37
39.5	16	21	2	28		5	5	17	1	7	3	1	7	3	30	10	15
40.0	6	8	2	8		8	3	18	1		1		4		17	4	5
40.5	1	7	2	4	1	12	4	24		3	2		3		12	4	2
41.0	1	1	1	6		7	2	22	1	2			2		4	3	1
41.5		1	2	4		7		18		1	1		2		2	3	1
42.0		5	1	2		5		8		2			1		2	3	1
42.5	2	3	1			3		8								1	1
43.0		6				1	2	3					2		1	2	
43.5				2		1		4									2
44.0	1	2		3				1	1							2	
44.5	1	4	1	3				4						1	6	3	
45.0	2	3	5	1		1		5							4	6	1
45.5	3	4	2	6				2					1		5	9	2
46.0	1	4	3	4		1		3	1	2			1	1	1	4	4
46.5	2	1	2	1				3		1					3	6	1
47.0	2	5	3	7		2			1	2	1		1		2	12	1
47.5	1	3	2	3				2		1			2		3	2	2
48.0	1	1		3						2	1		1			2	
48.5	1	1		1											1	2	
49.0	1	1	1	1				1	1	1	1					2	
49.5		3	1					1		1			1			1	
50.0				2											1		1
50.5																	1
51.0																1	
51.5															1		
Total	420	960	140	720	20	80	20	220	20	60	40	60	380	40	700	240	460

[1] All subareas.
[2] Includes 60 fish not classified by subarea.
[3] Includes 40 fish from subarea P.
[4] Includes 120 fish from subarea Q.

TABLE 21.—*Length frequency of mackerel in May and June 1926 to 1935, inclusive, by time periods and by statistical subareas*—Continued

Length, centimeters	May 1927												June 1927								
	1–10				11–15	16–20		21–31					1–5				6–10				
	A	B[5]	C	D	B	Q	S	A	O	P	Q[6]	S	O	P	Q	S	A	O	P	Q	S
<33.0									1												
35.0			1	1																1	
35.5			1	1																	
36.0		2	3	1														2		3	1
36.5		6	9	4	2						1	1							1	4	2
37.0	1	13	45	5	5	1	1	1			4	2		1	8	1	2	1	1	23	2
37.5		56	87	26	21	4	5	2			12	7	2		23			5	3	48	6
38.0	4	148	190	31	36	13	4	9	1		32	8		1	49	1	3	14	10	102	11
38.5	2	173	221	69	54	8	14	3	1	1	46	19	3		87	2	6	29	4	122	15
39.0	3	207	197	72	44	14	10	6	1	2	61	20	3	2	99	1	6	28	3	161	18
39.5	4	149	172	45	28	11	11	3	4	1	74	16	12		112	2	1	35	8	124	8
40.0	6	110	104	31	24	13	8		4	7	116	18	11	3	124	5	1	37	3	95	9
40.5	2	57	55	10	10	13	2	5	12	6	155	19	16	3	147	6	1	31	1	41	5
41.0		25	23	7	1	11	6	5	6	12	202	12	23	3	135	8		26		39	1
41.5	2	13	14	3	2	9	7	2	11	7	164	17	19	3	96	6		14	1	22	2
42.0		5	7	3		2	3	2	7	6	113	9	12	3	56	2		12	2	8	
42.5		1	4	4		2	2		4	7	50	6	4		37	2		6	1	7	
43.0		2	1	2	1		2		2	1	41				16			3	1		
43.5		1				4				1	22		3		9			2		3	
44.0		1	2	2	2		2				21	2	1		4			1			
44.5		1	2		1	2	1			2	16	2			6			1		1	
45.0		3	5	1	1	8	2	1	1	2	21	2			2			2		2	
45.5		5	11		1	8	2		1	1	31	4	3	1	14			2		3	
46.0		4	5			1	2				18	3	1		5	1		1	1	4	
46.5		4	3	2	2	1	4				34	3	1		7	1		5		1	
47.0		2	4		1	3	2			1	25	3	3		7			1		2	
47.5	1	1	2		3	5	4				17	4	1		6			1		1	
48.0	1	2	3			2	2	1	3	2	15	1	1		3	1				2	
48.5		1	2			3	2			1	11	1			3	1		1		1	
49.0			1			1	1				7				1						
49.5							1		1		6				1						
50.0		2				1					3				2						
50.5											2	1									
51.0															1						
51.5					1								1								
Total	26	994	1,174	320	240	140	100	40	60	60	1,320	180	120	20	1,060	40	20	260	40	820	80

Length, centimeters	June 1927										
	11–20						21–30				
	A	O	P	Q	R	S	D	P	Q[7]	R	S
<33.0									3	1	
34.5											1
35.0									4	1	
35.5								1	1	1	
36.0	1	2		2		1		1	3	1	3
36.5		8		5		2		1	7	3	3
37.0	2	18	1	24		4		5	47	4	9
37.5	13	51	2	75	1	12		7	103	12	24
38.0	19	88	8	119	7	26		15	199	11	44
38.5	29	136	9	190	2	48	3	19	234	16	47
39.0	19	170	21	199	2	41	1	13	251	27	37
39.5	15	172	22	143	3	47	5	13	193	15	14
40.0	15	147	14	57	1	23	7	2	99	18	13
40.5	3	102	7	36	1	12	5	1	33	5	2
41.0	3	47	8	13		10	4	2	11	3	2
41.5		33	2	8	2	2	4		4	1	
42.0	1	17	1	2		2	4		2		
42.5		8					2		1		
43.0		8	2	1		1	1				
43.5		7			1		1				
44.0		9	1			1	1				
44.5		6					2				
45.0		9	1	2		1					
45.5		12		2		3			1		
46.0		14				1			1	1	1
46.5		13									
47.0		8		1		1			1		
47.5		3		1					1		
48.0		3									
48.5		7							1		
49.0		1									
49.5						1					
50.0						1					
51.0		1	1								
Total	120	1,100	100	880	20	240	40	80	1,200	120	200

[5] Includes 39 fish for which the subarea was not reported.
[6] Includes 20 fish for which the subarea was not reported.
[7] Includes 60 fish for which the subarea was not reported.

TABLE 21.—*Length frequency of mackerel in May and June 1926 to 1935, inclusive, by time periods and by statistical subareas*—Continued

Length, centimeters	May 1928									June 1928										
	1–10		11–20		21–31					1–2		5–10		11–20				21–30		
	B	C	A	B	A	B	P	Q	R	P	Q	P	Q	O	P	Q	R	O	P	Q
20.5	----	----	----	1	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
21.5	----	----	----	2	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
22.0	----	----	----	5	----	----	----	----	----	----	----	----	----	----	----	1	----	----	----	----
22.5	----	----	----	5	----	----	----	----	----	----	----	----	----	----	----	2	----	----	----	----
23.0	----	----	----	9	----	----	----	----	----	----	----	----	----	----	----	4	----	----	----	----
23.5	----	----	----	5	----	----	----	----	----	----	----	----	----	----	----	7	----	----	----	----
24.0	----	----	----	4	----	----	----	----	----	----	----	----	----	----	----	11	----	----	----	----
24.5	----	----	----	1	----	----	----	----	----	----	----	----	----	----	----	6	----	----	----	----
25.0	----	----	----	2	----	----	----	----	----	----	----	----	----	----	----	5	----	----	----	----
25.5	----	----	----	1	----	----	----	----	----	----	----	----	----	----	----	3	----	----	----	----
26.0	----	----	----	1	----	----	----	----	----	----	----	----	----	----	----	3	----	----	----	----
27.0	----	----	----	2	----	----	----	----	----	----	----	----	----	----	----	1	----	----	----	----
36.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	1
36.5	----	----	1	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
37.0	----	----	----	----	2	1	----	----	----	----	----	----	2	----	1	2	1	----	----	----
37.5	----	----	2	2	2	1	----	----	1	----	----	----	----	----	1	5	----	----	5	5
38.0	6	1	2	15	8	3	----	2	----	----	1	4	5	----	10	34	----	----	9	17
38.5	9	1	17	60	21	8	----	10	2	2	7	5	20	4	34	76	----	7	19	58
39.0	25	2	37	166	37	20	2	13	15	----	8	11	51	4	61	200	8	16	47	148
39.5	39	3	46	193	99	20	3	18	18	2	21	32	89	12	106	285	3	22	81	232
40.0	43	3	64	276	112	26	3	25	27	4	17	17	82	12	100	325	3	39	97	224
40.5	32	4	67	250	109	21	5	36	33	3	27	21	78	6	72	233	2	30	77	177
41.0	21	2	47	167	82	20	11	36	37	1	22	9	51	2	63	116	1	14	41	103
41.5	12	2	26	99	64	11	5	44	31	----	31	9	21	----	19	70	2	6	30	53
42.0	1	----	11	52	28	3	9	26	16	3	22	5	7	----	8	26	----	3	11	13
42.5	3	----	7	20	20	2	11	13	17	2	16	3	7	----	3	13	----	----	1	2
43.0	1	1	4	10	15	1	2	20	7	----	13	3	2	----	1	5	----	----	----	1
43.5	1	----	3	4	11	----	3	6	13	----	5	1	1	----	----	1	----	1	----	2
44.0	----	1	1	5	4	2	1	4	7	1	1	----	----	----	----	3	----	1	2	----
44.5	2	----	----	3	5	----	1	2	3	2	3	----	----	----	----	2	----	----	----	----
45.0	----	----	3	5	7	----	----	5	6	----	----	----	----	----	----	1	----	----	----	----
45.5	1	----	2	10	6	----	----	3	5	----	----	----	----	----	----	----	----	----	----	----
46.0	2	----	3	5	4	----	----	3	5	----	----	----	2	----	----	----	----	----	----	1
46.5	1	----	5	9	5	1	1	4	9	----	----	----	1	----	1	1	----	----	----	1
47.0	1	----	1	16	5	----	2	3	8	----	1	----	1	----	----	2	----	----	----	----
47.5	----	----	1	15	3	----	----	1	9	----	2	----	----	----	----	----	----	----	----	----
48.0	----	----	3	4	4	----	----	3	1	----	2	----	----	----	----	----	----	----	----	1
48.5	----	----	4	3	2	----	----	----	8	----	----	----	----	----	----	----	----	----	----	----
49.0	----	----	1	3	3	----	1	----	7	----	1	----	----	----	----	----	----	----	----	1
49.5	----	----	1	1	2	----	----	----	1	----	----	----	----	----	----	----	----	----	----	----
50.0	----	----	----	1	----	----	----	1	1	----	----	----	----	----	----	----	----	----	----	----
50.5	----	----	1	----	----	----	----	1	1	----	----	----	----	----	----	----	----	----	----	----
51.0	----	----	----	----	----	----	----	1	1	----	----	----	----	----	----	----	----	----	----	----
51.5	----	----	----	1	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
52.0	----	----	----	1	----	----	----	----	----	----	----	----	----	----	----	----	----	1	----	----
Total	200	20	360	1,434	660	140	60	280	289	20	200	120	420	40	480	1,443	20	140	420	1,040

TABLE 21.—*Length frequency of mackerel in May and June 1926 to 1935, inclusive, by time periods and by statistical subareas*—Continued

Length, centimeters	May 1929							June 1929														
	1–10				11–20		21–31	1–10		11–15			16–20						21–30			
	A	B	C	D	A	B	A	O	Q	D	E	Q	E[8]	E[9]	H	O	Q	R	E	G[10]	H	O
19.5		5																				
20.0		6																1				
20.5		8																1				
21.0		3																				
21.5		3																3		1		
22.0		1																7				
22.5																		12		6		
23.0																		22		2		
23.5																		35		6		1
24.0																		40		9		2
24.5																		22		26		1
25.0			1															9		36		1
25.5			4															5		26		2
26.0			9															2		25		3
26.5			17				2											2		5		1
27.0			22	1			3													3		
27.5			18	3			2											2		4		
28.0			7	2			3													3		
28.5			6															1		7		1
29.0																		2		18		2
29.5			1				1											1		29		7
30.0																				46		5
30.5																				25		2
31.0																				18		
31.5																				4		
32.0																1						
32.5								1												2		
33.0									1											2		
33.5			3	1					1			1							1			
34.0			7						2			5								2		
34.5			9				1		4			4								1		
35.0			13	2			2		3			5				1	6		2	6		1
35.5			7						15			13		2		1	2		3	6		1
36.0		1	5					1	11			17	1	1		2	1		1	14	1	4
36.5			3				1		12			15		2		1	1		2	10	1	
37.0								1	8			9				1	3		2	11	1	1
37.5									7			6				1	1		1	4		1
38.0			1						3			6		1						10		
38.5			2				1		2											3		
39.0	1	3	4				1		4			5	1			3	2			3	1	2
39.5	4	5	18		1	5	5		13			14				2	6		5	8		6
40.0	6	25	74	1	4	5	9		31	2	4	38	1	1		13	13		13	20	2	10
40.5	14	64	93	1	8	10	27	2	101		2	68	4	1	1	21	22		32	65	9	20
41.0	32	101	130	3	18	12	38	2	176	2	8	111	9	4	5	47	46		58	87	11	44
41.5	27	110	120	2	29	14	44	10	194	2	13	107	12	7	1	42	56		62	116	8	38
42.0	33	110	88	3	26	23	59	5	186	10	12	117	10	7	4	45	49		74	121	15	41
42.5	26	76	58	5	29	8	33	14	132	7	13	62	11	4	6	22	24		60	108	12	17
43.0	15	64	53	5	18	6	31	15	70	3	13	23	21	2		9	14		38	64	7	10
43.5	6	29	18		7	8	17	12	20	1	10	14	4	2	3	5	6		12	29	6	1
44.0	2	20	7		6	4	10	4	14	2	2	5	7	1		1	3		7	18		
44.5	2	7	1	1	5	2	4	6	3		3		3	2	1	1	1		6	5	1	2
45.0	1	4	2		2	1	5	1	5		2		1	1			2		2	5		
45.5	3	5			1		2	2	1	2	3		3			1	1		2	3	1	
46.0	1	6	2		2	1	2	1	1				2				1		2	7	1	1
46.5	1	4	1				1				1		1		2		2			2	2	
47.0	2	5			1		2	1	4		2		1	1			4		2	5	1	
47.5		7	1				2		3		1					3			1	2		
48.0	2	3	2				1		1	1	1	1			1	1	1		1	1		
48.5		5						1	2				1				1		1	2		
49.0		1			1				1			1	2						1	4		
49.5	1	4			1	1		1			2	1										
50.0	1	2			1		1												1			
50.5		1					1															
51.0			1												1							
53.0									1					1								
Total	180	688	808	30	160	100	311	80	1,032	32	92	648	95	40	25	224	268	167	392	1,045	80	228

[8] June 17.
[9] June 19 and 20.
[10] Includes some samples from adjacent positions of subareas H and O.

TABLE 21.—*Length frequency of mackerel in May and June 1926 to 1935, inclusive, by time periods and by statistical subareas*—Continued

Length, centimeters	May 1930									June 1930											
	1–10			11–20				21–26	27–31	1–10			11–20			21–30					
	B	C	D	A	Q	R	S	Q	Q	Q	R	S	E	Q	R	E	G	H	O	P	Q
23.5														1							1
24.0														5							
24.5														6							1
25.0														11							2
25.5														16							11
26.0										1				12							3
26.5										1				13				1			5
27.0														2							3
27.5														6							5
28.0										1				4							2
28.5														2							1
29.0														6							
29.5														2	1						
30.0										2				1							
30.5														1			1				
31.0										1							1	2			
31.5																	1		1		
32.0										2				2							1
32.5										6				6							1
33.0									1	21				9		1	1				2
33.5									6	52				30			5		6		7
34.0								1	4	154	5			103			16	2	16	3	23
34.5									7	218	15			169		2	31	5	34	10	34
35.0									6	248	6			223		5	53	5	52	13	52
35.5									1	190	7			185		4	88	10	69	17	60
36.0						1				76	3		1	110		5	80	10	36	12	37
36.5										35	3			61		4	34	13	27	2	23
37.0				1	1			1	1	8	1			22		2	16	5	9	2	6
37.5										6	1			9		3	10	2	6	1	7
38.0				1	1					5				2	1	3	12	1	3		3
38.5						1				3	1			4		2	5	2	4		
39.0					1									2	1		5		2		1
39.5		1						1		3			1	2	3	2	2	2	1		
40.0		3						1		8		1		1	3		7	5	1		1
40.5	1	12		4	3		1	1		11			4	3	4	4	6	8	5		2
41.0	5	32		8	3	1				17	1	3	8	8	1	6	20	10	14		4
41.5	10	62	3	21	8	1		1	2	40	6	2	11	14	2	7	25	22	20		9
42.0	23	81	3	22	8			6	1	67	2	4	21	17	1	16	54	52	25		11
42.5	18	83	4	22	8	2	4	7	2	61	1	7	22	17	2	17	61	35	18		4
43.0	21	92	5	29	8	3	3	14	3	58	3	7	16	16		12	46	48	24		5
43.5	27	73	5	17	8	4	1	34	5	58		1	16	12		8	35	44	9		3
44.0	10	45	1	15	9		4	34	4	49		3	10	4		8	18	14	7		1
44.5	5	26	3	17	9	1	2	42	2	36			10	1	1	2	9	7			
45.0	8	13		6	5	3		34	1	28			3			6	6	2	3		
45.5		5		2	7	1	1	23	3	19		1	4			1	1	1			
46.0		1		1		1	1	14	1	8		1	2	1		5	4	1			1
46.5	1	4		1	2	1		9		6			3	1			1				2
47.0	1	3		1	5	2		4		4		2	1			1	2		2		
47.5	1	2			6	1	2	9		3								1			
48.0				3	8	1		4		2			1			2	1	1			
48.5					3	1		4		2	1					1					
49.0	1				6		1	4									1	1			
49.5		1	1					2					1						2		
50.0		1			2					5						1					
50.5		1								1											
51.0										1									1		
Total	132	541	25	171	111	25	20	250	50	1,517	56	32	135	1,122	20	130	658	312	397	60	334

TABLE 21.—*Length frequency of mackerel in May and June 1926 to 1935, inclusive, by time periods and by statistical subareas*—Continued

Length, centimeters	May 1931									June 1931											
	1–10			11–20			21–31			1–10			11–20			21–30					
	B	C	D[11]	A	B	Q	A	Q	S	O	Q	S	Q	R	S	G	H	O	P	Q	R
18.0											1										
19.0											1		1								
19.5											8										
20.0											4		5								
20.5											17		6								
21.0											5		8								
21.5											11		14								
22.0											11		4								
22.5											9		1								
23.0											4		1								
23.5											1										
24.0											3										
25.5																					1
27.0																					1
27.5																					1
28.0																					3
28.5																					6
29.0																					2
29.5																					2
30.0													1								4
31.5																				1	
32.0													1								
32.5													2								
33.0													4								
33.5			3										7							1	
34.0			2										21		1					3	
34.5			3					1				1	38							4	
35.0			3					1			6	1	58			1				14	
35.5			1								8		41				1			18	
36.0			2								10	1	40				1			11	
36.5			8					1			5		23			1	3		1	8	
37.0		1	17				1	3			5	1	14				2			7	
37.5			56				1	3			14		13							4	
38.0		2	90				2	5			58	1	19				3			4	1
38.5			110	1	1			28	1		68	2	22				6			18	
39.0		2	109	6	5	3	4	21	1		77	4	25	1			6		1	29	
39.5	1	1	88	6	2	2	3	39	1		80	5	34		2	1		1		32	
40.0		1	62	6	3	1	6	30	2	1	30		24		2	1	3			26	
40.5			42	4	3	1	3	13			26	9	19	1		3	9			25	6
41.0		3	51	8	12	4	2	4			20	8	31	3	3	2	5	3		32	4
41.5	1	3	43	19	14	5	9	9	6		44	23	60	4	13	1	9	3	1	61	4
42.0	5	10	76	42	53	10	8	17	9		56	34	104	3	5	7	26	5	2	100	2
42.5	4	11	88	64	47	12	14	20	7		76	30	161	14	3	13	25	8	5	108	2
43.0	8	10	100	73	73	13	16	18	12	1	93	34	152	9	4	10	27	15	4	142	
43.5	13	5	73	92	78	9	11	22	8	2	74	29	104	7	3	8	26	12	1	102	
44.0	5	4	71	75	70	12	13	29	11	4	44	20	82	3		7	16	5	2	66	
44.5	3	2	47	55	32	12	10	25	10	6	30	10	40	4	1	3	11	4	1	41	
45.0	2	3	33	38	34	9	3	17	8	5	15	4	13		3		5	2		10	
45.5	3	1	18	19	13	3	3	16	5	5	14	4	9	1		1	5	2		3	
46.0			13	15	4	4	6	11	7	6	4		1							5	1
46.5	1		6	6	2	1	3	5	2	3	3	1	1				1			1	
47.0	1		4	6	1	3	2	2	5	3	4		2			1					
47.5		1	4	5	3	1			3		2	2	2							2	
48.0	1		2	7	3	1	1	2	2	1			2								
48.5	1		1	9	4	2	2	3	2	1	3		2								
49.0	1		3	3	1			1		1										2	
49.5			1		1			3											1		
50.0				4		1		1		1			2						1		
50.5				1	1			1				1									
51.5				1																	
Total	50	60	1,230	565	460	109	123	351	102	40	944	225	1,214	50	40	60	190	60	20	880	40

[11] Includes 40 fish for which subarea was not reported.

TABLE 21.—*Length frequency of mackerel in May and June 1926 to 1935, inclusive, by time periods and by statistical subareas*—Continued

Length, centimeters	May 1932									June 1932												
	1–10				11–20			21–31		1–5			6–10			11–20		21–30				
	A	B	C	D	A	Q	R	O	Q[12]	O[12]	Q[12]	S	O[12]	Q	S	F	O	E	G	H	O	P
22.5				1																		
23.0			1												1							
23.5															1							
24.0			1											1								
24.5															2							
25.0				1										2	4			3	1			1
25.5			1							1					9			4				3
26.0			2	1								2		5	15			16	3		1	4
26.5			2	3						5		1		8	14			11			3	4
27.0			6	9					1	11				6	27			15	3		14	7
27.5			12	6					5	8		3	1	13	27			18	2		14	8
28.0			25	12					14	25			2	10	42			23	4		16	6
28.5			30	13					27	27		3	5	18	54			24	2		23	4
29.0			21	21					35	63	3	7	6	22	37			26	3		37	8
29.5			37	18					36	76		1	2	8	28			22			28	2
30.0			48	15				2	44	80	3	2	5	10	27	2		29			31	2
30.5			51	14				1	51	77	5	3		12	19	8		15	1		24	
31.0			47	15				3	32	69	4	1	1	8	16	9		13			11	1
31.5			36	12				9	30	51	7	1	2	6	10	5		9			13	
32.0			27	5			2	2	11	27	6			1	5	11		6	1		11	
32.5			18	3				8	7	9	6	1	1	3	1	2		2			3	
33.0			5	3				1	5	5	3			2	1	3		4			1	
33.5			2						3	4	1											
34.0		2	1	1					2		1											
34.5									2	1								1				
35.0				1							1											
35.5			1							1								1				
36.0									1				2				1					
36.5								1	1												1	
37.0			2							2							2					
37.5		1							1	1			3								2	
38.0		1	1				1	2	3	1			1	1	1		2				2	
38.5			3		1		2	2	7	3	1		4		1		5					
39.0			7			1	3	9	9	6	2		10	1	1		8		1		2	
39.5	1	3	12		4		3	12	23	16	1		8				16		2	1	5	
40.0	2	9	22		2	1	3	12	23	14	1		14	2	1		24	2		1	9	
40.5	3	14	18		4	3	1	13	20	11	2		7	1	2		44	1		1	11	
41.0	1	16	21		7	1	1	13	5	16	2		10	3	2		30	2			11	
41.5	4	19	31		6	2		3	7	13			15	4	4		26	2	2		20	
42.0	6	46	63		18	2		2	3	26	2		12	7	11		46	1	1	2	23	
42.5	9	63	104		28	2		2	5	28	8		20	7	9		63	1	1	2	46	
43.0	11	98	134		38	2	1	2	8	29	13		21	21	15		81		4	4	45	
43.5	15	112	99		38	5	1	4	15	51	15		28	16	11		86	3	3	3	49	
44.0	14	100	87		35	10		6	17	50	21		24	13	15		68			3	45	
44.5	7	69	62		28	8	1	7	14	59	10		19	8	5		43	1	4	2	23	
45.0	3	46	28		22	10		7	16	48	3		14	6	6		26	2		1	22	
45.5	2	16	17		12	7		3	13	48	2		5	2	3		16				6	
46.0	1	10	5		9	5	1	1	10	27	3		4	2			7		1		2	
46.5		2	2		2	4		1	8	25	3		3				2				2	
47.0	1	4	3		1	3		1	1	10	3		4		1		1	1			1	
47.5			1		2	2			2	6	1		1				2	1			1	
48.0		4	1		1	1		1	2	5	1				1							
48.5		2	1			1		2	4	5	1						1	1	1			
49.0		1							1	6											2	
49.5		1			1			1	1	2					1							
50.0					1			1		3				1								
50.5										4			1									
Total	80	639	1,098	154	260	70	20	134	525	1,055	135	25	255	230	430	40	600	260	40	20	560	50

[12] 1 sample of 25 large fish taken on May 31 is omitted from the May 21–31 column and included in the June 1–10 column.
[12] 2 samples of 65 large fish taken on June 6 are included with the June 1–5 and excluded from June 6–10 column.

TABLE 21.—*Length frequency of mackerel in May and June 1926 to 1935, inclusive, by time periods and by statistical subareas*—Continued

Length, centimeters	May 1933							June 1933									
	1–10			11–15	16–20	21–25	26–31	1–10			11–20			21–30			
	B	C	D	B	Q	Q	Q	E	O	Q	E	O	Q	E	G	O	Q
29.0	1																
29.5	1	2	1								1						
30.0	1	2	3						2	2							
30.5		4	6					1	10	5	3	3	5				
31.0	1	12	8			1	1		27	9	1	6	4	1	1		
31.5	2	13	14			1	8	1	60	27	5	15	14	17	1	5	1
32.0	7	17	14			4	5	1	62	36	11	32	39	25	9	10	3
32.5	3	26	11			2	6	1	101	34	27	26	39	48	10	9	5
33.0	5	34	19		1	11	4	6	74	23	24	17	45	63	26	9	2
33.5	9	28	14		3	6	4	3	62	22	12	13	22	64	20	5	2
34.0	3	35	11	1	1	10	2	1	51	12	13	8	10	56	13	4	2
34.5	5	26	5	3	2	3	4	1	40	15	11	6	6	41	7	2	2
35.0	3	28	5	2	5	9	2	1	13	2	6	3	4	22	5	4	1
35.5	1	14	3		4	8	3		8	1	3	3		13	4	1	1
36.0	3	13	4	1	2		1		8	4	3	1	1	4	4	1	1
36.5		11	1	1	3	5		1	2	1				4		1	
37.0		4	1		1	1		3	2								
37.5				1	2			2	2		1			2			
38.0		1				1			5	1	1		2	2			
38.5	1				3				2			1		1			
39.0	2	5							3	1	2	1		4	1	1	1
39.5	1	3		1	1	1			3	3	2	3	2	1		1	1
40.0	4	4		2	3				10	1		3	2	3		4	
40.5	4	7		5	3				6	3	1	12	3		2	7	2
41.0	10	15		1	3	2			8	3	1	8	6	5	1	9	1
41.5	7	13		2	5	3		2	21	10	1	29	7	12		8	1
42.0	7	26		7	2	1			26	15	2	25	7	14		15	3
42.5	6	26		5	2	3		1	49	24	6	48	7	30	4	20	4
43.0	10	40		17	5	3			39	15	6	72	23	35	3	36	5
43.5	6	48		14	8	2		2	54	23	3	64	12	25	3	35	9
44.0	6	36		14	5	5		1	29	13	4	53	18	19	1	33	7
44.5	4	40		10	4	3		1	30	14	3	43	11	16	5	17	4
45.0	4	26		12	12	4			19	7	4	28	9	10		15	1
45.5	2	18		5	11	9			9	1	2	14		5		3	
46.0	2	6		3	12	4			6	5		7	1	3		1	
46.5	3	3			3	4			2	2		2		1		1	
47.0		1		2	1	2		1	3					3		1	
47.5	1	1			2				1			2				1	
48.0		3				1			3			2					
48.5	1	1								1	1			1		1	1
49.0		2			1	1							1				
49.5		1		1					1								
Total	126	595	120	110	110	110	40	30	853	335	160	550	300	550	120	260	60

TABLE 21.—*Length frequency of mackerel in May and June 1926 to 1935, inclusive, by time periods and by statistical subareas*—Continued

Length, centimeters	May 1934												May 27–June 2		June 1934									
	1–5		6–12			13–19					20–26				3–9	10–16				17–23		24–30		
	B	C	A	B	C	A	B	Q	R	S	O	Q	O	Q	Q	E	G	O	Q[14]	E	Q	E	G	Q
25.5																	1		1		1			
26.0																	1							
26.5																					1			
27.5																		1						
28.5					1																			
29.0																			1					
29.5					1										1		1							
30.0					2										1		1	3	2		1			
30.5					3										2		2	1	9					
31.0					1			1							7		3	3	8		1		1	
31.5					5							1		2	12		4	13	16	1	3		1	2
32.0		1			6									3	23	1	6	11	38	3	5		3	5
32.5		1		1	2								1	4	40		8	16	34	2	7		4	4
33.0					3							1		7	18		4	9	28	1	12		9	5
33.5		3			3			1						5	16	1	6	6	35	1	9		8	6
34.0		14		7	12	3	3	2	1				1	9	15	3		8	19	1	10		5	8
34.5		23		32	30	12	8	5		1		5		20	8			4	11	1	15	1	8	7
35.0		45	2	51	70	17	14	11	1	2	5	12	4	52	40	2		10	31	4	33		10	26
35.5		59	5	91	124	26	16	29	4	3	10	26	5	99	86	6	1	16	62	12	60		30	49
36.0		76	7	100	141	46	23	42	9	1	17	51	8	155	115	10		28	54	14	83	6	32	92
36.5	1	71	4	99	136	42	7	31	1	5	19	106	10	160	149	9		27	78	16	75	4	46	80
37.0		42	1	54	108	49	15	34	2	5	27	95	8	138	119	12	1	18	43	8	52	3	41	67
37.5		21	3	30	38	30	9	20	4	3	10	63	8	82	61	14		22	20	9	25	4	22	35
38.0		10	2	15	23	14	6	9	3		10	49	2	55	58	13	1	8	6	6	12	2	9	15
38.5		6		6	7	11	1	9			3	26	1	19	13	4		3	3	4	4	1	4	10
39.0		1		11	10	4	2	5		2	8	16	2	15	4	6		3		3	4			3
39.5		4	1	9	5	3	3	12		1	2	6	1	6	6	1		3	1	3	2			1
40.0	4	11	1	14	12	6	5	7	1		8	13	1	13	1	3		1		2	2		1	2
40.5	1	10	6	19	20	18	2	12	2	2	8	19	1	18	6	4		2		1	4	1	1	2
41.0	2	14	11	26	32	19	8	12	2		13	26	1	16	11	3				2	5	1	3	11
41.5	6	16	11	54	32	22	6	17	1		18	50	2	18	10	2		6	2	6	16	1	2	7
42.0	7	15	10	67	19	25	10	19	3		11	21	1	23	19	3		4	3	2	25	1	3	24
42.5	11	23	17	94	13	38	14	18	6		10	22	2	29	26	7		8	4	4	49		11	35
43.0	7	21	18	145	15	48	26	42	2	1	5	18	1	39	33	5		12	7	11	60	6	12	55
43.5	9	36	23	153	27	58	33	31	4		4	51	2	52	62	5		14	11	12	86	2	10	56
44.0	10	28	26	177	23	51	40	54	7	2	8	71	6	63	58	8		17	11	16	74	2	13	55
44.5	10	14	22	145	19	52	24	65	5		11	65	3	62	56	7		17	3	4	72	2	8	46
45.0	21	12	16	106	19	56	22	56	6	1	20	60	3	58	40	4		12	4	5	36	2	2	34
45.5	6	10	9	56	5	37	13	48	5	1	18	73	2	56	26	2		8	3	11	17	1	6	12
46.0	2	2	4	24	3	24	8	30	5	1	10	50	3	25	16	1		2	1	2	10		2	6
46.5	1			14	7	14	4	30	3		12	45	1	26	6	1		2		2	2		1	
47.0	2			10	3	8	8	9	2		6	31		12	5	3		1		1				
47.5		1		1		2		10			3	11		13	3									
48.0			1			2		6			3	11		7	1			1					1	
48.5								1				5		4										
49.0				2		1		2				6												
49.5				3					1		2	3		4									1	
50.0												2		1	2									
50.5						1		1																
51.0					1	1																		
Total	100	590	200	1,616	981	740	330	681	80	31	281	1,110	80	1,370	1,175	140	40	320	550	170	872	40	310	760

[14] 1 special, nonmarketed, sample of 30 small fish from area Q on June 13 not included.

TABLE 21.—*Length frequency of mackerel in May and June 1926 to 1935, inclusive, by time periods and by statistical subareas*—Continued

Length, centimeters	May 1935							June 1935						
	1–10	11–20			21–31			1–10	11–20	21–30				
	B	A	B	Q	B	Q[15]	S	Q[16]	Q	E[17]	G	H	Q	R
25.0									1					
25.5									1					
26.0										1				
26.5													1	
27.0								2		2				
27.5								1	2	1				
28.0								1					2	
28.5									1	1				
29.0										1				
31.0								9	2	1			1	
31.5								20	7	3				
32.0								54	46	21	1	2	2	2
32.5						3	3	98	76	49		1	11	3
33.0						2	1	132	132	115	3	5	11	4
33.5						8	2	109	154	120	3	4	11	12
34.0						7		108	148	143	1	6	4	6
34.5						8	2	65	82	115	4	7	2	8
35.0						8	3	28	48	82	1	5	2	4
35.5	2			1		9		23	13	30	3			1
36.0	2					27	1	41	14	17			3	
36.5	15		1	1	1	68	3	68	17	18	1			
37.0	51	4			5	152	12	123	34	25	2	2		1
37.5	138	7	11	2	6	201	13	179	54	46	4	6		
38.0	288	11	19	1	7	268	18	229	95	92	3	6		
38.5	382	10	21	5	4	229	25	214	102	104	5	6		4
39.0	407	16	20	6	2	143	22	147	102	148	2	5		
39.5	274	7	24	6	4	97	20	91	60	101	1	4		4
40.0	171	4	20	3	3	50	3	51	27	76	1	4		
40.5	86	4	9	1	1	24	4	18	12	32		1		
41.0	47	1	9	3	1	28	6	13	2	36		2		
41.5	51	8	5	1		27	5	6		25	2			
42.0	89	9	7	3		32	8	11	13	27		1		
42.5	100	5	11	2	1	26	10	10	7	33		1		
43.0	181	10	13	2		26	10	19	29	50	2			
43.5	208	14	22	1	6	42	13	37	23	63	3		1	
44.0	257	22	42	2	3	37	12	29	29	80	3	2		1
44.5	246	24	37	2	1	43	15	18	29	61	3	1		
45.0	214	12	32	1	3	44	16	17	23	49		1		1
45.5	153	10	25	1	1	54	7	15	12	57	2	3		
46.0	97	8	15			30	5	14	7	28		1		
46.5	43	2	10	4		22	6	5		11				
47.0	19	1	2		1	9	4	5		5				
47.5	4	1	2	1		5	1			2				
48.0	1		3			7				1				
48.5	2			1		5		1						
49.0						1			1	1				
49.5	1							2		1				
50.0							1							
Total	3,529	190	360	50	50	1,742	251	2,013	1,405	1,874	50	76	51	51

[15] Includes 90 fish for which the subarea was not reported.
[16] Excludes 66 small (less than 26 centimeters) fish taken June 6 and 7.
[17] Includes some fish from area G.

TABLE 22.—*Numbers of individuals measured in samples of catches in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*

1926

Date	By purse seines				By drift-gill-nets
	D	E	G	P	E
Sept. 1			80		
Sept. 2		60	40		
Sept. 3		300	80		
Sept. 7		80	140		
Sept. 8		60	80		
Sept. 9			60		
Sept. 10			100		
Sept. 11		80	40		
Sept. 13		20	180		
Sept. 15		80			
Sept. 16		60			
Sept. 17		140	20		
Sept. 23			80		
Sept. 24	20		60		
Sept. 25			20		
Sept. 27		40			
Sept. 28	20	160	140		
Sept. 29		280	40		
Sept. 30		80	260		
Oct. 1			300		
Oct. 2			100		
Oct. 4			40		
Oct. 5			420		
Oct. 6			140	20	
Oct. 9			140		
Oct. 11			20		
Oct. 13					
Oct. 14			40		
Oct. 15		140	40	40	
Oct. 28		180	20		
Oct. 29		60			
Oct. 30		40	40		
Nov. 1		80			
Nov. 2		80			
Nov. 3		40			
Nov. 4		40			
Nov. 5		40			
Nov. 6		40	40		
Nov. 8		40	240		
Nov. 9			160		
Nov. 11			80		
Nov. 15			240		
Nov. 29			100		
Nov. 30			120		60
Dec. 1					80
Dec. 11					193

1927

Date	By purse seines					By drift-gill-nets
	E	G	H	O	P	E
Sept. 1		100				
Sept. 2		220				
Sept. 6	100	80	20			
Sept. 7		200	40			
Sept. 8		120		20		
Sept. 14	40	120			40	
Sept. 15	20	60				
Sept. 17		100				
Sept. 19		100	20		20	
Sept. 20			100			
Sept. 22	160	100				
Sept. 23			160			
Sept. 24		40	40			
Sept. 26			140			
Sept. 27			80			
Sept. 28			90			
Sept. 29			200			
Oct. 4			260			
Oct. 5			140			
Oct. 8			100			
Oct. 17						100
Oct. 18	180					
Oct. 27	80					100
Oct. 28	120	100				
Nov. 3		100				

TABLE 22.—*Numbers of individuals measured in samples of catches in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued.

1927

Date	By purse seines					By drift-gill-nets
	E	G	H	O	P	E
Dec. 12						180
Dec. 13						40
Dec. 14						140
Dec. 15						80
Dec. 16						120
Dec. 17						160
Dec. 19						80
Dec. 22						180
Dec. 23						260
Dec. 24						20

1928

Date	By purse seines					By drift-gill-nets
	E	G	H	P	Q	E
Sept. 4			100			
Sept. 6	20		40			
Sept. 7			140			
Sept. 10	40		140			
Sept. 14			40			
Sept. 20			100			
Sept. 22		285				
Sept. 24		40		80		
Sept. 25			40	180		
Oct. 5					90	
Oct. 10					80	
Oct. 22						60
Nov. 9						190
Nov. 14						80
Nov. 15						620
Nov. 16						460
Nov. 19						160
Nov. 22						360
Nov. 23						130
Nov. 26						60
Nov. 30						120
Dec. 3						20
Dec. 4						200
Dec. 5						80

1929

Date	By purse seines				By drift-gill-nets
	D	E	G	H	E
Aug. 23			105	60	
Aug. 24			20		
Aug. 26			239		
Aug. 27			210		
Aug. 28			141		
Aug. 30			140		
Sept. 16	40		39		
Sept. 18		20			
Sept. 19		30			
Sept. 23					60
Sept. 27		15			
Sept. 30		11			
Oct. 7		29			
Oct. 21					100
Oct. 22					110
Nov. 4					30
Nov. 5					215
Nov. 6					162
Nov. 7					220
Nov. 8					160
Nov. 13					210
Nov. 14					223

TABLE 22.—*Numbers of individuals measured in samples of catches in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued.

1930

Date	By purse seines								By drift-gill-nets
	C	D	E	G	H	O	P	Q	E
Aug. 11		245		90					
Aug. 12		100					40		
Aug. 14				30			100		
Aug. 15				20		70	126		
Aug. 16				20		20	60		
Aug. 18			80	80			45		
Aug. 19			20			40	20	100	
Aug. 20						48	56		
Aug. 21							40		
Aug. 29							60		
Aug. 30							20		
Sept. 2				40					
Sept. 3			40	20		20			
Sept. 8		210							
Sept. 12			25						
Sept. 15			40						
Sept. 16					45				
Sept. 17			65						
Sept. 20				80					
Sept. 22				20					
Sept. 23				60					
Sept. 24				200					
Sept. 26				20			40		20
Sept. 29							100		
Sept. 30							40		
Oct. 1							294		
Oct. 13									30
Oct. 16									20
Oct. 24			126						58
Oct. 29									60
Oct. 31									103
Nov. 3									140
Nov. 4									140
Nov. 5									120
Nov. 10									150
Nov. 11									80
Nov. 12									40
Nov. 14									214
Nov. 20									40
Nov. 21									390
Nov. 22									195
Nov. 24									153
Nov. 28									60
Nov. 29									80
Dec. 1									210
Dec. 3									80
Dec. 4									140

1931

Date	By purse seines				By drift-gill-nets
	C	D	E	G	E
Aug. 11	60	20			
Aug. 12	60				
Aug. 13	100				
Aug. 15	40				
Aug. 17	105	120			
Aug. 18	140	40			
Aug. 19	100	20			
Aug. 22	140				
Aug. 24	220				
Aug. 25	230				
Aug. 26	20	100			
Aug. 27	140				
Aug. 28	20	80			
Aug. 29	40				
Aug. 31	40				
Sept. 1	75				
Sept. 4	20				
Sept. 8	130				
Sept. 9	160				
Sept. 10	180				
Sept. 11	250		40		
Sept. 21	190	40			
Sept. 22	80				
Sept. 23			200		
Sept. 24			140		
Sept. 28			80		

TABLE 22.—*Numbers of individuals measured in samples of catches in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued.

1931

Date	By purse seines				By drift-gill-nets
	G	D	E	G	E
Oct. 6			120		
Oct. 13		60	40	62	
Oct. 17				180	
Oct. 22			30		40
Oct. 23					160
Oct. 27					20
Nov. 10					50
Nov. 12					70
Nov. 15					120
Nov. 16					455
Nov. 17					70
Nov. 18					90
Nov. 22					20
Nov. 23					110
Nov. 24					240
Nov. 25					60
Nov. 28					20
Nov. 29					40
Nov. 30					170
Dec. 1					90
Dec. 3					100
Dec. 4					40
Dec. 7					120

1932

Date	By purse seine			By drift-gill-nets
	C	D	E	E
Aug. 11	20			
Aug. 12	20	20		
Aug. 13	240			
Aug. 15	140			
Aug. 16	60	40		
Aug. 17		20		
Aug. 18	20			
Aug. 20		40		
Aug. 22	83			
Aug. 23		146		
Aug. 24		40		
Aug. 25		94		
Aug. 26		51	56	
Aug. 27		47		
Aug. 30		70		
Aug. 31		100		
Sept. 1		60		
Sept. 8			140	
Sept. 9		40		
Sept. 12			40	
Sept. 19		20	20	
Sept. 20		20		
Sept. 21			20	
Sept. 27				22
Sept. 28		17		
Sept. 30		47		20
Oct. 1		20		
Nov. 7				110
Nov. 12				20
Nov. 14				55
Nov. 15				80
Nov. 16				250
Nov. 17				160
Nov. 18				120
Nov. 21				200
Nov. 22				120
Nov. 23				80
Nov 25				160
Nov. 26				120
Nov. 29				105
Nov. 30				60
Dec. 2				280
Dec. 5				70
Dec. 6				140
Dec. 7				100
Dec. 8				50
Dec. 9				140
Dec. 10				30
Dec. 14				43

TABLE 22.—*Numbers of individuals measured in samples of catches in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued.

1933

Date	Purse seines	By drift-gill-nets	Date	Purse seines	By drift-gill-nets
	E	E		E	E
Aug. 28	220	------	Oct. 19	120	------
Aug. 29	218	------	Oct. 20	80	------
Aug. 30	140	------	Oct. 21	40	------
Aug. 31	180	------	Oct. 22	140	------
Sept. 1	65	------	Oct. 24	180	------
Sept. 5	160	------	Oct. 27	270	------
Sept. 6	336	------	Oct. 28	120	------
Sept. 7	90	------	Oct. 30	110	------
Sept. 8	100	------	Oct. 31	210	40
Sept. 9	120	------	Nov. 1	40	------
Sept. 11	60	------	Nov. 2	70	90
Sept. 12	20	------	Nov. 4	------	60
Sept. 13	160	------	Nov. 6	------	40
Sept. 14	180	------	Nov. 7	------	120
Sept. 15	30	------	Nov. 10	------	20
Sept. 20	100	------	Nov. 17	------	100
Sept. 21	290	------	Nov. 18	------	80
Sept. 22	220	------	Nov. 20	------	235
Sept. 23	160	------	Nov. 21	------	160
Sept. 25	120	------	Nov. 22	------	440
Sept. 26	140	------	Nov. 23	------	150
Sept. 27	100	------	Nov. 24	------	40
Sept. 28	230	------	Nov. 25	------	20
Sept. 29	110	------	Nov. 27	------	100
Sept. 30	160	------	Nov. 28	------	60
Oct. 2	180	------	Nov. 29	------	340
Oct. 3	160	------	Dec. 1	------	260
Oct. 4	220	------	Dec. 2	------	35
Oct. 9	180	------	Dec. 4	------	26
Oct. 10	280	------	Dec. 5	------	235
Oct. 11	380	------	Dec. 6	------	189
Oct. 12	170	------	Dec. 7	------	70
Oct. 13	40	------	Dec. 8	------	190
Oct. 14	100	------	Dec. 9	------	40
Oct. 16	280	------	Dec. 11	------	35
Oct. 18	140	------	Dec. 14	------	40

1934

Date	By purse seines				By drift-gill-nets
	D	E	G	H	E
Sept. 21	100	50	------	------	------
Sept. 22	------	140	------	------	------
Sept. 24	------	20	80	------	------
Sept. 25	------	------	261	------	------
Sept. 26	------	210	------	------	------
Sept. 27	------	100	------	------	------
Sept. 28	------	------	223	------	------
Sept. 29	------	40	40	------	------
Oct. 1	------	141	------	------	------
Oct. 5	------	------	108	100	------
Oct. 6	------	40	------	------	------
Oct. 8	------	40	------	------	------
Oct. 11	------	200	------	------	------
Oct. 13	------	40	------	------	------
Oct. 15	20	------	------	------	------
Oct. 17	------	240	------	------	------
Oct. 18	------	145	------	------	------

TABLE 22.—*Numbers of individuals measured in samples of catches in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued.

1934

Date	By purse seines				By drift-gill-nets
	D	E	G	H	E
Nov. 13	------	------	------	------	190
Nov. 18	------	------	------	------	97
Nov. 19	------	------	------	------	273
Nov. 20	------	------	------	------	100
Nov. 21	------	------	------	------	135
Nov. 26	------	------	------	------	167
Nov. 28	------	------	------	------	126
Nov. 30	------	------	------	------	60
Dec. 5	------	------	------	------	61

1935

Date	By purse seines				By drift-gill-nets
	E	O	Q	R	E
Sept. 3	229	------	105	------	------
Sept. 4	100	------	217	------	------
Sept. 5	116	------	------	------	------
Sept. 9	87	------	50	------	------
Sept. 10	60	------	------	------	------
Sept. 11	74	------	------	------	------
Sept. 12	127	------	------	------	------
Sept. 13	35	------	------	------	------
Sept. 18	348	------	------	------	------
Sept. 19	68	------	------	------	------
Sept. 20	116	70	------	------	------
Sept. 23	73	63	------	------	------
Sept. 24	------	177	------	------	------
Sept. 25	267	241	------	------	------
Sept. 26	------	543	------	------	------
Sept. 28	75	------	------	------	------
Sept. 30	------	------	149	------	------
Oct. 1	393	------	------	------	------
Oct. 2	83	------	50	------	------
Oct. 3	332	------	195	------	------
Oct. 4	------	------	319	------	------
Oct. 5	331	------	------	------	------
Oct. 7	246	------	------	------	------
Oct. 17	180	------	------	------	------
Oct. 19	364	------	------	------	------
Oct. 21	------	------	458	------	------
Oct. 22	------	------	194	------	------
Oct. 24	------	------	910	------	------
Oct. 26	------	------	375	------	------
Oct. 28	------	------	378	------	------
Oct. 29	------	------	760	158	------
Oct. 30	------	------	751	59	------
Oct. 31	------	------	------	146	------
Nov. 4	------	------	588	------	58
Nov. 9	------	------	455	------	------
Nov. 12	------	------	------	------	163
Nov. 20	------	------	------	------	119
Nov. 22	------	------	------	------	240
Nov. 26–29	------	------	------	------	1,292
Dec. 2–4	------	------	------	------	796
Dec. 11–13	------	------	------	------	668
Dec. 16–17	------	------	------	------	266

TABLE 23.—*Length frequencies of mackerel in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*

1926

Length, centimeters	Purse seines																	Drift-gill-nets	
	September—							October—							November—			Nov. 30 to Dec.1	Dec.11
	1–10		11–20		21–30			1–10		11–20			21–31		1–10		11–20	21–30		
	E	G	E	G	D	E	G	G	P	E	G	P	E	G	E	G	G	G	E	E
31.0			1																	
31.5		1																		
32.0			2			1	1													
32.5	1		2	1		2	1													
33.0	4		1			4	1	3												
33.5			1	1		4	3	2												
34.0	1			1		5	2	1												
34.5		1	3	1		4		1	1						1					
35.0	9	3	4	1		7	1	3			1									
35.5	10	5	6	5		20	4	16		1										
36.0	28	14	13	11	1	25	14	22	2	2	1									
36.5	29	30	31	11	4	39	30	69		3	6		1							
37.0	39	69	40	24	2	61	57	120	4	3	6	4					1			
37.5	53	115	42	55	6	89	99	210	3	7	14	9	8	1	2	2	1			
38.0	74	109	65	59	8	98	125	256	5	16	23	7	11	2		5	2			
38.5	74	103	72	32	9	84	122	202	2	24	14	10	15	4	15	13	9	1		
39.0	73	72	44	28	7	73	76	127	2	17	18	6	31	8	30	29	6	5	2	1
39.5	39	34	27	6		21	26	50		15	8	2	45	9	23	53	33	9	7	2
40.0	31	14	13	1	2	13	16	24		14	3	2	53	9	58	71	38	19	6	9
40.5	14	5	3	1		5	9	7		14	2		35	9	70	81	55	26	19	9
41.0	4	1	3			1	6			7	2		29	11	62	73	65	34	17	16
41.5	4	1	4	2		1	1	3	1	3			29	1	49	50	39	31	30	9
42.0	3	1	1			1	1	2		6	1		8	3	21	29	29	25	19	5
42.5						1	1	2		1			7	3	8	10	12	8	7	7
43.0							1	1		3			3		7	9	4	4	5	8
43.5							1	1		2			1		4	5	2	4	3	3
44.0	1							1		1					1	1	1	5	2	7
44.5	1							2							3		2	2	3	13
45.0	2							2					1		2	2	5	7	3	13
45.5	1		1					2								1	3	8	6	15
46.0					1		1	2		1					2	2	5	13	2	20
46.5	1							1					1		1	1	2	8	5	23
47.0	1												1		1		3	4	1	14
47.5		1				1		1					1			3	2	3	1	7
48.0	2						1	1										2	1	3
48.5								5									1	1		3
49.0	1																			4
49.5		1						1			1								1	
50.0			1																	2
51.0																		1		
Total	500	580	380	240	40	560	600	1,140	20	140	100	40	280	60	360	440	320	220	140	193

TABLE 23.—*Length frequencies of mackerel in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued

1927

Length, centimeters	Purse seines																Drift-gill-nets			
	September—											October—				Nov. 1–10	October—		December—	
	1–10			11–20					21–30			1–10	11–20	21–31			11–20	21–31	11–20	21–31
	E	G	H	O	E	G	H	P	E	G	H	H	E	E	G	G	E	E	E	E
32.0	2																			
32.5	1					1														
33.0	5	1				1			1											
33.5									1											
34.0	2																1			
34.5	1																			
35.0						1			1											
35.5		1							2											
36.0	1	1				1					1									
36.5	5	4			1	2			1	3	4									
37.0	2	17	3	1	1	7		3	4	3	6	6	1							
37.5	8	33	2		1	18	5	4	6	10	21	22								1
38.0	11	73	2	2	6	33	15	6	9	16	75	47	4	2	2	1	1			
38.5	16	93	9	5	7	62	16	6	11	20	121	71	2	2	6	1	4	2		
39.0	11	127	18	1	11	65	26	9	18	26	174	113	12	9	3	2	4	2	2	5
39.5	12	122	15	4	7	67	28	11	20	24	133	93	16	17	5	4	8	4	3	2
40.0	9	92	4	6	4	60	17	5	20	17	80	75	16	24	12	6	10	5	12	15
40.5	7	65	2	1	11	31	8	5	26	7	57	37	20	31	13	10	7	11	26	32
41.0	2	34	1		2	10	4		6	4	19	14	26	25	10	15	17	14	67	49
41.5	2	15	1		2	9		3	6	2	9	6	26	26	15	18	16	19	98	63
42.0	2	9	1		2	4	1	1	8	2	3	6	21	34	15	18	9	17	110	64
42.5		5			1	1		1	3		1	1	11	17	5	10	10	10	99	46
43.0		5	1		1	3		2	5	2		1	17	5	6	5	5	5	75	31
43.5		5			1				3	2	1		4	2		6	5	4	48	16
44.0	1	2							2		3	3	2	3	2	2	2	3	38	9
44.5		4			2				2				1	1	1	1	1	2	22	12
45.0		3				1		1	1	1		1		1	1				20	6
45.5		1				1			3						2				23	20
46.0		2						1			1	1			1			1	28	24
46.5		2				1													37	22
47.0		1						1	1			2							36	21
47.5						1					1	1	1					1	23	7
48.0		2								1									14	2
48.5								1											8	4
49.0			1												1				4	1
49.5		1												1		1			1	4
50.0																				2
50.5																			5	
51.0																			1	1
52.0																				1
Total	100	720	60	20	60	380	120	60	160	140	710	500	180	200	100	100	100	100	800	460

1928

Length, centimeters	Purse seines							Drift-gill-nets				
	September—						Oct. 1–10	Oct. 21–31	November—			Dec. 1–10
	1–10		11–20	21–30					1–10	11–20	21–30	
	E	H	H	G	H	P	Q	E	E	E	E	E
37.0				1			1					
38.0				3		2	1					
38.5		1		5	1	4	4					
39.0	1	8	2	15		9	6					
39.5	2	19	8	32	4	27	23		1	2		
40.0	6	72	23	53	6	50	26		2	5	4	
40.5	1	94	27	52	10	39	31	1	2	24	6	1
41.0	8	66	27	44	9	37	44	5	8	45	14	4
41.5	4	73	16	35	4	31	11	6	5	85	32	5
42.0	6	47	18	28	3	21	7	6	23	116	66	15
42.5	8	16	8	16		12	6	8	31	184	96	31
43.0	4	8	6	12	1	2	4	9	34	201	107	43
43.5	2	3		5		1		7	31	209	84	33
44.0	2			2	1	2	2	6	20	166	81	42
44.5	5	3		4		4	1	4	13	98	58	25
45.0	2	1	1	2	1	3	1	4	8	60	28	23
45.5	3	1		4		2		3	4	22	22	9
46.0		2	1	2		2	1		1	25	13	11
46.5			1	1		2	1			18	14	6
47.0	1	1	1	4		2			3	14	10	12
47.5	1	1		2		3			2	21	16	12
48.0	2	2						1		8	5	11
48.5		1	1	2					1	7	8	7
49.0	1	1		1		1			1	5	5	3
49.5	1					1				1	1	4
50.0						2				2		
51.0										2		2
51.5												1
54.0						1						
Total	60	420	140	325	40	260	170	60	190	1,320	670	300

TABLE 23.—*Length frequencies of mackerel in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued

1929

Length, centimeters	Purse seines							Drift-gill-nets			
	August—		September—				Oct. 1–10	Sept. 21–30	Oct. 21–31	November—	
	21–31		11–20			21–30				1–10	11–20
	G	H	D	E	G	E	F	E	E	E	E
30.0										1	
32.5	1										
33.0	5										
33.5	2										
34.0	6										
34.5	4										
35.0	6										
35.5	1					1					
36.0	10					1				1	
36.5	29		1			1			1		
37.0	48	1			1	1					
37.5	73	1				1					1
38.0	70	1	3		1	2	5	1	2	3	
38.5	46	1	2		1		1	2	1	5	
39.0	33		3	6	1	2	2		1	9	
39.5	23		3	3	1		2	1	5	13	2
40.0	37	2	1	2	3			5	3	10	2
40.5	74	3	1	1	2		3	1	2	7	1
41.0	73	10	6		3	1			1	8	4
41.5	90	5	3	1	4		1	4	7	15	6
42.0	81	7	6	10	9	3	3	5	8	36	23
42.5	42	5	6	2	3	2		8	16	57	37
43.0	28	4	2	3	2	2	4	8	28	95	51
43.5	25	4	1	4	2	4	1	4	28	120	65
44.0	7			5		1	2	3	28	125	71
44.5	5	3	1	2	1	1	1	2	25	99	61
45.0	6					1	2	5	15	91	48
45.5	1	2		5		2	1	3	19	40	32
46.0	4	1		2	1			2	6	20	11
46.5	5			3	1		1	1	8	12	6
47.0	3	2	1	1	1			3	3	8	3
47.5	3	2			1			1	2	6	6
48.0	3	1							1	3	3
48.5	4	3			1						
49.0	5							1		2	
49.5		2									
51.0	1										
52.0	1									1	
Total	855	60	40	50	39	26	29	60	210	787	433

TABLE 23.—*Length frequencies of mackerel in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued

1930—BY PURSE SEINES

Length, centimeters	August—							September—									October—	
	11–20						21–31	1–10				11–20			21–30		1–10	21–30
	D	E	G	O	P	Q	P	D	E	G	O	E	G	H	G	P	P	E
30.0																	1	
30.5			1		2												3	
31.0																	2	
31.5			1		1							1					2	
32.0		1	2		2							1					2	
32.5			2		3					1		3					6	
33.0			4		4							7			1		4	
33.5			2		5							7					4	
34.0			3		5		1			2		9			4	1	5	
34.5			7	2	5					1		6	1			1	2	
35.0		2	4	1	18			1		2	1	3	1		2	1	6	1
35.5	1	2	20	9	45	4	7	1	1	3		2	1		3	2	6	
36.0	2	4	37	22	66	13	18	5		6	1	6	4	3	5	10	18	1
36.5	12	5	42	36	101	20	21	8		14	4	6	8	3	10	18	35	2
37.0	11	21	46	43	93	26	32	20	2	14	2	4	18	5	25	39	61	6
37.5	13	19	24	27	54	20	25	33	3	6	5	12	13	8	28	41	52	5
38.0	9	13	12	15	20	12	9	33	10	7	3	12	11	11	29	25	36	7
38.5	5	8	9	11	13	3	5	25	8	3	2	5	15	8	33	17	26	19
39.0	3	8	4	3	4	1		17	6		1	9	6	5	27	9	12	9
39.5	1	1	3		1			3	4		1	6		2	17	4	2	4
40.0	2	2	2	1	1			4	2			1			10	1	2	7
40.5	7	1	1					1				2			1	1	3	1
41.0	8		3	2	1			1				1			8	2	2	1
41.5	11	1	6	1	1				1	1		3			5	4	2	3
42.0	24	2	1	2			1	3	1			1	1		11	2		4
42.5	32	1			1							1			14	1		7
43.0	26	3	1	1				2	1			4			10			10
43.5	41					1	1	7				3	1		12			11
44.0	33	3	1	1				3				3			9			10
44.5	25	1	1		1			5	1			4			7			5
45.0	21	1		1				9				4			5	1		4
45.5	9							4							5			3
46.0	19							5				1			3			3
46.5	4							8							4			1
47.0	9	1						2							4			
47.5	6							2				1			1			1
48.0	2							5							5			1
48.5	4											1			2			
49.0	3							1										
49.5												1						
50.0			1					1										
50.5								1										
51.0	1																	
51.5	1																	
Total	345	100	240	178	447	100	120	210	40	60	20	130	80	45	300	180	294	126

1930—BY DRIFT-GILL-NETS (SUBAREA E)

Length, centimeters	Sept. 21–30	October—		November—			Dec. 1–10
		11–20	21–31	1–10	11–19	20–30	
34.0	1			1			
34.5					1		
35.0			2				
35.5			1				
36.0			2			2	
36.5		2	2	4	4	4	
37.0		6	11	17	18	10	3
37.5	1	1	11	24	34	31	7
38.0	2	5	22	62	41	33	9
38.5	1	5	18	76	45	54	15
39.0		4	11	48	49	47	10
39.5	1	4	4	21	19	18	9
40.0		2	3	12	5	19	3
40.5		1		8	7	9	2
41.0		1	3	5	8	9	
41.5			2	6	4	10	3
42.0	2	1	9	31	9	23	8
42.5	1	5	13	22	11	30	10
43.0	2	3	11	29	9	33	29
43.5		1	18	35	9	64	47
44.0		2	14	40	21	92	45
44.5	1	2	19	31	9	98	68
45.0	1	2	20	34	9	109	56
45.5	7	1	9	16	6	84	30
46.0		1	10	15	5	51	20
46.5			1	7	7	26	15
47.0		1	4		3	19	15
47.5			1	2		21	4
48.0				1	1	10	5
48.5				1		3	5
49.0						5	2
49.5				1		2	
50.0				1		1	2
50.5							2
51.0							2
51.5						1	2
52.0							1
52.5							1
Total	20	50	221	550	334	918	430

TABLE 23.—*Length frequencies of mackerel in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued

1931

Length, centimeters	Purse seines															Drift-gill-nets			
	August—				September—						October—					Oct. 21-30	November—		Dec. 1-10
	11-20		21-31		1-10	11-20		21-30			1-10	11-20			21-30		10-20	21-30	
	C	D	C	D	C	C	E	C	D	E	E	D	E	G	G	E	E	E	E
30.5																	1		
32.5														1		1			
33.0								1		1									
33.5															1				
34.0							1								1				
34.5											1			1	1				
35.0	1		1	1				1			2								
35.5	2	1	3					1			1			2					
36.0	3		3	2	1									2	2				
36.5	4	1	13	2	5	1		2		1	4		1	2	1				
37.0	7	2	17	1	11	2		2	1	4	3	2	1	1	1			2	
37.5	6	5	17	2	7	4		5		1	2	1			1		4		1
38.0	21	4	26	10	17	4		4	2	8	5	2	1	6		2	8	2	2
38.5	29	9	38	16	33	12	2	17		16	10	4		22		1	14	9	3
39.0	54	21	100	19	59	24	3	36	7	48	12	1	2	33		2	34	11	4
39.5	60	30	109	26	85	38	8	33	8	54	16	11	3	33	4	8	45	22	10
40.0	66	23	112	21	96	35	8	41	3	65	14	10	6	50	8	5	84	33	24
40.5	47	25	78	23	49	23	2	29	6	60	9	7	9	31	2	11	65	33	19
41.0	21	6	36	12	33	15	2	26	3	44	10	1	3	12	2	5	56	22	8
41.5	12	9	24	2	19	9	4	6	1	20	4		3	6		4	29	13	4
42.0	22	9	21	4	10	7	1	5	1	17	3	2	3	6		16	10	14	3
42.5	27	7	26	4	22	12		5	2	10	4			4		29	17	11	2
43.0	39	10	32	8	17	9	1	8		11	5	4		3	1	26	23	24	8
43.5	41	14	46	5	23	9	1	4	1	17	1	2	3	5	2	29	48	23	13
44.0	42	4	44	7	23	13	2	9	1	10	5	1		5		31	69	38	28
44.5	26	6	34	3	15	8	2	4	2	9	4	5	1	5		13	75	62	41
45.0	29	4	29	5	12	7		11	1	5	2	3	3	4		16	74	99	42
45.5	16	2	16	1	11	4	1	10		5		2		6		10	87	90	39
46.0	14	4	18	1	5	8		3		3	1		1	2	1	2	38	52	39
46.5	5		1	3	4	2	1	3	1	7	1	1				1	37	38	28
47.0	2	1	3	1	1	2		1		3	1	1			1	3	18	27	9
47.5	3	1	2		2	1		1		1					1		5	20	11
48.0	3	2	1	1		2										3	9	4	4
48.5	1			1												1	4	4	1
49.0	2				1	1	1	1								1	1	3	3
49.5																		2	
50.0																		2	3
50.5					1														1
51.0								1											
52.0					1														
Total	605	200	850	180	565	250	40	270	40	420	120	60	40	242	30	220	855	660	350

TABLE 23.—*Length frequencies of mackerel in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued

1932

Length, centimeters	Purse seines											Drift-gill-nets					
	August—					September—						Sept. 21–30	November—			December—	
	11–20		21–31			1–10		11–20		21–30 [1]			1–10	11–20	21–30	1–10	11–20
	C	D	C	D	E	D	E	D	E	D	E	E	E	E	E	E	E
33.0				1													
34.0																1	
34.5															1		
35.0		1		1	1									3	1		1
35.5				1		1									2	1	
36.0				1										1			
36.5	1	1		1											2		
37.0				2									1	1		1	
37.5				2													1
38.0	1			1					2		1			3	1		
38.5	2	2		5		1	1		2	1			2		2		
39.0	10	4	1	11	1	1		3	2	3			3	5	8		
39.5	9	7	1	21	3	2	1	4	4	3		2	5	12	17	5	
40.0	22	8	1	32	2	7	5	1	7	8	1	2	12	38	34	14	1
40.5	33	11	6	38	8	7	9	5	6	11		3	15	59	63	25	2
41.0	43	14	6	52	3	5	14	3	6	5	1		12	50	68	21	1
41.5	27	8	6	40	4	7	7	1	2	1	4	4	10	48	46	28	
42.0	25	9	8	35	2	11	8	1	2	5	4	1	6	36	36	20	3
42.5	39	3	8	47	5	4	11	7	4	1		3	4	24	23	20	1
43.0	40	13	7	55	8	11	23	3	3	11	3	1	5	37	24	26	1
43.5	61	8	11	40	2	9	14	4	9	11	1	4	7	30	33	34	2
44.0	54	14	11	56	9	10	15	4	1	8	3	4	6	39	62	60	6
44.5	43	6	8	49	4	5	15	1	4	5	1	5	7	61	80	99	3
45.0	32	5	3	24	1	11	5	2	2	1	1	7	7	49	94	104	4
45.5	27	2	3	15		2	6		2	6		1	3	53	92	97	7
46.0	16	3	1	11	1	2	1	1	1	4		3	3	50	59	84	3
46.5	5		1	3	1	2	2						2	36	37	65	3
47.0	4	1	1	2			1		1			1		15	24	38	2
47.5	4			1	1	1						1		9	15	22	
48.0						1	2							6	13	13	2
48.5	1			1										7	4	10	
49.0														7	3	6	
49.5	1													2	1	10	
50.0														1		3	
50.5														1		2	
51.0														1			
51.5														1		1	
Total	500	120	83	548	56	100	140	40	60	84	20	42	110	685	845	810	43

[1] Includes 1 sample of 20 mackerel landed Oct. 1 from subarea D.

TABLE 23.—*Length frequencies of mackerel in the fall, 1926 to 1935 inclusive, by gear, by time periods, and by statistical subareas of area XXII*—Continued

1933

Length, centimeters	Purse seines										Drift-gill-nets							
	Aug. 27 to Sept. 2	September—				October—				Oct. 29 to Nov. 4	Oct. 29 to Nov. 4	November—				December—		
		3–9	10–16	17–23	24–30	1–7	8–14	15–21	22–28			5–11	12–20	21–25	26–30	1–5	6–10	11–14
32.0	1		1															
32.5	3	5					3		2	1								
33.0	11	14	2	4	5	3	6	7	16	2								
33.5	30	31	14	8	20	8	21	22	22	6		1						
34.0	69	55	30	30	45	32	67	62	57	11	6	6	1	1				
34.5	99	94	58	68	70	53	119	99	98	13	5	4		2				
35.0	126	111	70	128	162	96	192	137	126	24	11	10	5	10			1	
35.5	102	108	69	144	192	122	256	116	129	19	18	13	10	11	1		1	
36.0	67	65	64	117	134	106	183	95	81	12	16	9	13	12	2		2	
36.5	42	54	32	107	115	75	136	56	52	7	25	12	13	22	6	1	2	1
37.0	19	16	19	64	57	30	65	24	38	6	25	15	18	8	8	3	9	
37.5	11	3	6	23	25	22	29	10	9	4	11	9	9	17	6	8	16	
38.0	3	2	4	8	9	4	10	10	7		9	8	9	16	5	4	12	
38.5	3	2	4	9	3	4	4	1	1		6	4	6	4	8	6	6	
39.0	4	1	1	1			3		1	1	7	2	1	7	5	6	5	
39.5	1	3	2	1	1				1		1	2	6	15		2	5	
40.0	1	6	2	1	1		2				1	4	18	20	4	4	11	
40.5	6	2	1	1	1		3				3	3	23	46	9	10	11	
41.0	12	17	3	1	1						6	9	32	53	12	15	12	1
41.5	12	18	6	3	1		1				11	3	38	72	20	17	22	1
42.0	24	27	10	3	1		6				3	7	26	56	18	25	26	5
42.5	35	21	13	6			2				2	6	24	52	18	29	24	4
43.0	38	30	8	6	3		4		1		3	12	21	47	17	21	18	4
43.5	34	27	5	7	2		7				7	6	19	41	24	44	36	4
44.0	26	33	9	13			4				2	6	22	54	37	48	38	13
44.5	24	24	3	6	3		5				4	5	30	52	49	59	40	11
45.0	10	19	7	5	4		4				2	6	24	61	64	64	61	9
45.5	3	6	4	2	2		3				1	1	17	43	52	67	41	5
46.0	3	5	2	1								2	13	38	34	31	21	6
46.5		1		1			1					5	9	21	42	32	26	1
47.0		1			1								3	11	28	25	13	4
47.5		2		2								1	4	4	10	17	11	3
48.0													1	6	5	7	2	
48.5	1	1													4	5	5	3
49.0														2	6	2	5	
49.5														1	3	3	6	
50.0														1	1	1		
50.5															1		1	
51.0															1			
Total	820	804	449	770	858	555	1,136	639	641	106	185	171	415	806	500	556	489	75

TABLE 23.—*Length frequencies of mackerel in the fall, 1926 to 1935 inclusive by gear, by time periods, and by statistical subareas of area XXII*—Continued

1934

Length, centimeters	Purse seines								Drift-gill-nets		
	September—			October—					November—		Dec. 5
	21–30			1–10			11–20		13–21	26–30	
	D	E	G	E	G	H	D	E	E	E	E
29.0			1								
29.5									1		
30.5									2	2	
31.0								2	7	1	
31.5									7	5	
32.0					1	1		2	19	3	
32.5	1			2		1		3	4	2	
33.0			1	4				4	8	1	
33.5		3	1					8	2	1	
34.0			5	4		2	1	10	4	1	
34.5		14	1	7	1	1	2	38	3	1	
35.0	5	16	13	6	5	4	3	67	9	1	
35.5	5	41	24	25	9	10	2	115	9	2	3
36.0	5	46	19	28	13	10	5	91	27	4	1
36.5	7	62	52	24	15	13	3	81	35	7	4
37.0	10	71	60	23	18	16	2	61	47	13	7
37.5	12	68	41	24	14	11		36	75	23	6
38.0	17	59	68	18	13	11	1	29	107	41	4
38.5	7	35	43	21	7	4	1	27	90	30	5
39.0	9	38	38	8	4	5		27	65	25	
39.5	5	19	31	12		2		5	38	11	3
40.0	1	12	17	2	2	1		4	26	2	4
40.5	2	8	13	6	1	1		2	21	16	3
41.0	2	3	12	1		1			17	15	4
41.5	1	14	17	1		1		3	23	24	
42.0	1	8	18	1				1	29	27	1
42.5	1	9	18		1	1			32	16	
43.0	1	3	25			2		1	23	14	2
43.5	2	3	24		2			2	14	8	2
44.0	1	6	14	1					14	10	3
44.5	2	9	14	2				3	11	6	1
45.0	2	7	16	1					9	11	4
45.5	1	4	9		1	2			4	13	
46.0		2	5					2	5	6	1
46.5					1			1	3	5	2
47.0			2						1	1	1
47.5									2	2	
48.0									1		
48.5			2								
49.0									1		
49.5										1	
Total	100	560	604	221	108	100	20	625	795	353	61

TABLE 23.—*Length frequencies of mackerel in the fall, 1926 to 1935 inclusive by gear, by time periods, and by statistical subareas of area XXII*—Continued

1935

Length, centimeters	Purse seines													Drift-gill-nets				
	September—							October—					Nov. 1–10	November—			December—	
	1–10		11–20		21–30			1–10		11–20	21–31			1–10	11–20	21–30	1–10	11–20
	E	Q	E	O	E	O	Q	E	Q	E	Q	R	Q	E	E	E	E	E
23.0										1								
25.0											1							
26.0											1							
27.0						1												
27.5						5					1							
28.0					2	11		1		1	1							
28.5					6	26	4	1	4	1	11		2			1		
29.0					19	38	12	1	8	3	33		1					
29.5					37	55	16	14	11	10	77		5					
30.0	1			1	41	57	28	11	10	19	209		20					
30.5	2				47	62	26	25	9	45	300	3	30					
31.0		4	6		67	50	17	38	16	58	374	6	37					
31.5	7	3	7		39	43	17	38	12	75	346	5	40					
32.0	7	6	24	2	33	31	9	45	8	70	238	2	43					
32.5	9	9	30	2	14	14	5	35	8	53	139	5	21					
33.0	18	6	24		9	11	1	27	6	22	101	3	15					
33.5	17	14	26		2	23	1	16	10	9	63	5	11					
34.0	43	43	43	1	3	37	1	30	33	12	102	10	20					
34.5	91	66	69	9	8	58	2	35	81	12	211	20	57					
35.0	113	72	131	15	23	126	3	95	88	11	305	47	92					
35.5	105	72	132	18	12	110	3	119	91	23	393	70	114			2		
36.0	71	39	91	11	18	113	3	153	80	36	302	70	112		2	1		
36.5	38	21	79	5	12	86	1	135	40	22	189	34	86	2		4	2	1
37.0	26	2	40	2	3	32		100	21	10	107	14	40	1	3	36	6	6
37.5	5	5	13		3	12		53	4	6	42	8	25	2	11	73	11	11
38.0	3	1	11	1	1	5		52	6	4	50	7	33	5	19	112	38	25
38.5	5	2	7	1	1	3		53	1	5	41	11	41	7	33	242	81	51
39.0	2	2	8	2	6	4		68	3	8	59	11	42	6	45	290	116	112
39.5	4	2	10		2	3		49	3	5	31	12	20	9	43	257	104	93
40.0	2		6		1	1		38	2	4	18	4	19	3	39	180	73	100
40.5	1		1		1	1		27		1	7	1	17	4	15	95	46	62
41.0	2		2			1		15		4	4	1	4	3	8	38	27	47
41.5								11	1		5		5	3	9	39	31	59
42.0	1		1			1		6		1	8	1	4	2	7	28	42	51
42.5		1	3		1	1		14		2	3	2	6	2	5	24	56	59
43.0	2		2					10	2	2	8	3	15	1	7	29	36	45
43.5	1		2					9		3	10		19	1	14	16	31	51
44.0	5	1						15	4	3	8	4	13	2	6	16	18	30
44.5	5					3		9	1		10	1	12	1	2	15	14	29
45.0	4							6			9		12	1	5	7	22	28
45.5	2	1			1			15		2	7	1	3	2		11	12	20
46.0								8		1	2		4	1	5	6	14	28
46.5					1			7				2	3		4	2	8	9
47.0					1			1								3	4	10
47.5																5	2	5
48.0																	1	1
48.5																	1	
49.0					1													1
52.0									1									
Total	592	372	768	70	415	1,024	149	1,385	564	544	3,826	363	1,043	58	282	1,532	796	934

TABLE 24.—*Length composition of mackerel during the "summer" period, 1926 to 1935*

Length, centimeters	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935
	July 1–Aug. 31	July 1–Aug. 31	July 1–Aug. 31	July 1–Aug. 20	July 1–Aug. 10	July 1–Aug. 10	July 1–Aug. 10	June 25–Aug. 26	July 1–Aug. 20	July 1–Aug. 31
30.5							393			
31.0							472	3		
31.5							392	23		
32.0							423	50		129
32.5							293	153	123	146
33.0	2						219	337	163	317
33.5	18				9		137	605	268	700
34.0	32				32	2	101	974	347	1,170
34.5	45	2		4	60	7	45	1,055	410	1,438
35.0	74	3		10	169	13	38	998	575	1,416
35.5	115	6	1	8	342	29	12	763	653	971
36.0	186	21	3	12	572	52	7	537	816	528
36.5	431	76	5	27	680	72	10	248	958	260
37.0	759	233	13	49	612	89	15	150	1,142	135
37.5	1,325	541	27	43	375	77	14	67	888	158
38.0	1,642	1,146	67	41	222	81	4	26	770	238
38.5	1,477	1,843	223	24	129	69	13	23	484	302
39.0	860	2,124	571	20	85	107	10	27	379	324
39.5	394	1,717	1,089	56	40	135	16	19	175	255
40.0	183	1,118	1,791	203	46	146	31	23	125	174
40.5	64	495	1,832	482	109	158	60	23	110	110
41.0	33	227	1,470	841	205	119	58	30	70	57
41.5	20	87	961	1,003	367	182	53	43	97	38
42.0	15	31	505	1,023	674	319	67	66	120	49
42.5	10	18	207	669	684	448	79	100	161	101
43.0	3	13	91	386	614	485	92	118	221	115
43.5	4	9	53	157	457	422	101	119	259	154
44.0	2	8	18	74	263	319	109	104	279	183
44.5	6	12	25	33	103	175	74	91	214	156
45.0	7	11	12	23	45	82	38	69	163	141
45.5	1	7	13	18	28	36	19	23	73	93
46.0	6	8	16	24	14	24	11	20	43	68
46.5	3	9	12	16	8	11	2	7	22	22
47.0	3	7	15	16	24	9	5	6	10	9
47.5	1	4	19	12	12	3	2	2	9	3
48.0	3	5	15	9	23	8		3	5	1
48.5	1	4	6	4	12	2		4	3	1
49.0		2	6	3	10	4		2	1	1
49.5	4		2	3	4	1	1	1	1	2
50.0			3		8	2		1	1	
50.5			1		2		2			1
51.0				1	1					
51.5				1	2					
52.0	1				2	1				
Total	7,730	9,787	9,072	5,295	7,044	3,689	3,418	6,913	10,183	9,966

APPENDIX B.—MARKING EXPERIMENTS

In this section the data on experiments in marking mackerel will be given and their results discussed with special reference to the technique of the method.

Field experiments, begun prior to the inception of the comprehensive mackerel investigations,[1] soon revealed the difficulties in marking a species so active and so delicate as the mackerel, and subsequent endeavors sought to discover methods of marking that would be suited to the species. For convenience in reference, the experiments will be serially numbered and taken in approximately chronological order.

FIELD EXPERIMENTS

Experiment No. 1

In the spring and late fall of 1925 in the vicinity of Woods Hole, Mass., 696 mackerel were marked. The fish were caught in commercially operated pound nets, transferred to a live car, marked and released at the place they were caught. The tag used was a celluloid band commonly used in marking poultry. It consisted of a flat strip of celluloid molded in the form of a flat spiral of two complete turns forming a ring that was unwound, placed around the caudal peduncle and when released, resumed its original ring-shape surrounding the peduncle. The mackerel were measured to the nearest half inch before release. Returns from this experiment are given in table 25. Since the subsequent returns from individuals below and above 15¼ inches of length differed significantly, these sizes have been separated in the table. The individuals released August 24 to September 1 were all between 11 and 14 inches in length.

[1] These marking experiments took place under the auspices of the North American Council of Fishery Investigations in the United States and Canada. In the United States they began in June 1925, under the general direction of Henry B. Bigelow and the immediate supervision of William C. Schroeder. Late in that season supervision was transferred to O. E. Sette.

Table 25.—*Returns from 696 mackerel released in Buzzards Bay and Vineyard Sound, near Woods Hole, Mass., in 1925*

(EXPERIMENT NO. 1)

Time of recapture	June 8–17, under 15½ inches long (142 released)	June 8–17, over 15¼ inches long (415 released)	Aug. 24–Sept. 1 (139 released)
Local (area XXII S):			
0–4 days after release	1	2	3
5–9 days after release	1	1	
10–14 days after release		1	
14–19 days after release			1
20–24 days after release	1	1	
25–29 days after release	1		
30–39 days after release		1	
Total	4	6	4
Massachusetts Bay (area XXII E):			
July 11–20, 1925		3	
Sept. 12, 1925	1		
Oct. 7, 1925	1		
Total	2	3	
Lightship Grounds (area XXII O):			
July 13–20, 1925		2	
Rhode Island Shore (area XXII S):			
June 21–23, 1925	2	1	
July 2, 1925	1		
June 19, 1926		1	1
Oct. 19, 1926			1
Total	3	2	2
Western Long Island (area XXIII B):			
July 7, 1925	1		
Central Nova Scotia (area XXI M)		1	
Grand total	10	14	6

Experiment No. 2

During the summer and fall of 1925, at pound nets and weirs in the vicinity of Provincetown, Mass., 3,939 mackerel were marked. Procedure was the same as in experiment No. 1 except that the mackerel were transferred to a pocket of netting instead of a live car. The tag was identical to that used in experiment No. 1. The returns are given in table 26. Since relatively few (4 percent) of the Provincetown mackerel were above 15¼ inches in length, the sizes have not been separated in the table. However, there was a significant difference in the

percentage returns of the various sizes in this experiment. (See p. 350.)

TABLE 26.—*Returns from 3,939 mackerel released at Provincetown, Mass., during the summer and autumn of 1925*

(EXPERIMENT NO. 2)

Time and location of recapture	June 23–July 3 (949 released)	July 9–July 22 (1,294 released)	July 29–Aug. 5 (996 released)	Oct. 2–7 (700 released)	Total (3,939 released)
Southern Maine, area XXII D:					
Nov. 21, 1925	-------	1	-------	-------	1
Massachusetts Bay, area XXII E:					
0–4 days after release	28	57	55	29	169
5–9 days after release	16	4	3	-------	23
10–14 days after release	9	2	1	-------	12
15–19 days after release	2	1	-------	-------	3
20–24 days after release	2	-------	-------	-------	2
25–29 days after release	2	-------	-------	-------	2
30–59 days after release	3	-------	1	-------	4
60–89 days after release	2	1	-------	-------	3
90–120 days after release	2	-------	-------	-------	2
During first season, date uncertain	8	11	11	1	31
During second season—					
Aug. 2, 1926	-------	-------	1	-------	1
Aug. 28, 1926	-------	1	-------	-------	1
Sept. 8, 1926	-------	-------	-------	1	1
Total	74	77	72	31	254
Western side of South Channel, area XXII G: July 29 to Aug. 7, 1925	3	2	-------	-------	5
Southern Massachusetts, Area XXII R:					
June 8, 1925	1	-------	-------	-------	1
October 1926	1	-------	-------	-------	1
Total	2	-------	-------	-------	2
Rhode Island, Area XXII S:					
June 9, 1926	-------	-------	1	-------	1
Aug. 14, 1926	-------	1	1	-------	2
Total	-------	1	2	-------	3
Grand total	79	81	74	31	265

EXPERIMENT No. 3

In Casco Bay, Maine, 930 individuals were tagged August 4 to 25, 1925. Of these, 249 were caught in floating traps, and the procedure was the same as in experiment No. 2. The remaining 35 were caught by purse seine, 10 miles southeast of Seguin Island, and presumably were tagged immediately upon being brailed to the deck of the vessel. Otherwise, procedure, as well as the tag used, was the same as in previous experiments. Only four returns resulted from the trap-caught mackerel: One was caught locally, August 6, 1925; another, 10 miles southeast of Block Island, October 19, 1925; the third, 3 miles southeast of Fire Island, N. Y., June 7, 1926; and the fourth, off Point Judith, Newport, R. I., August 6, 1926. Of the purse-seine-caught mackerel one was recaptured 15 miles southeast of Eastern Point Light, Gloucester, Mass., August 2, 1926.

EXPERIMENT No. 4

To test the metal-strap tag of the type illustrated by Schroeder (1930, fig. 3), 90 individuals were tagged at Woods Hole, Mass. In this experiment the pound net was partially hauled to concentrate the mackerel which were dipped from the net, one at a time, tagged, and immediately returned to the water. The tag was the small size designated as No. 3 by its manufacturer, and it was attached at the base of the dorsal lobe of the caudal fin. Several tags were seen to have dropped off as the mackerel were returned to the water, and doubtless most of them did so later, for no returns resulted from this experiment, whereas other taggings of this size of mackerel at this season and at this place have yielded 13 percent returns. (If the stock at Woods Hole is such as to provide 13 percent returns with a suitable tag from a release of 90 individuals, there would be less than one chance in a thousand that no tags would be returned due to random causes alone.)

EXPERIMENT No. 5

To see whether the mackerel approaching the coast in early spring in the southerly end of the range were on their way to more northerly waters, 400 were marked (with the same style of tag as used in experiment No. 1) in the offing of Delaware Bay (lat. 37°35′ W.; long. 74°35′–40′ N.) April 10, 11, and 15, 1926. The fish were caught by commercial purse-seine fishermen and were tagged immediately after the fish were brailed to the deck of the fishing vessel. Of course, only the liveliest of the mackerel were selected for tagging, but even with severe selection the fish suffered more injury from this method of fishing and handling than those that were caught in pound nets and handled differently. At least this appears to be the most reasonable explanation of the paucity of returns from this experiment from which only two were recovered. One was from the same grounds on the day following tagging, the other was taken off Chatham, Mass. (area XXII G) the following August.

EXPERIMENT No. 6

To see whether better results might be obtained with an extremely light celluloid tag a special lot of tags was made of thin stock (0.025 inch thick) and with only one and a half turns. Thinking also that the bright cerise and yellow colors of the bands

previously used were likely to render their bearers more vulnerable to predators, the special bands were colored green. They were attached to 967 mackerel from pound nets in the vicinity of Woods Hole, Mass., July 15–27, 1927, using the procedure of experiment No. 2. A number of these mackerel were recaptured and released again shortly after the original tagging, so that the effective number released was 1,000. The releases and returns are given by sizes and by time-of-recapture groups in table 27. Returns from this experiment were so similar to those of experiment No. 2 that no substantial advantage of the modifications in the tag was indicated.

TABLE 27.—*Returns from mackerel tagged July 15–27, 1927, in the vicinity of Woods Hole, Mass.*

(EXPERIMENT No. 6)

Length when tagged, centimeters	Number tagged	Returns classified according to the number of days elapsed between release and recapture													
		0–4	5–9	10–14	15–19	20–24	25–29	30–34	55–59	60–69	70–79	80–89	90–99	Over 100	Sum
		Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
25.5	1														
26.5	3														
27.0	7														
27.5	6														
28.0	24	4													4
28.5	63	1	1		1								1		4
29.0	88	7	3	2		1									13
29.5	106	5	1	1								1			8
30.0	158	5	7	4		1				1			1	[1] 1	20
30.5	138	8	3	2	3	2	1		1	1	1				22
31.0	117	10	6	4	1							1			22
31.5	81	8	1	2										[2] 1	12
32.0	67	4	3						1						8
32.5	36	3	3		1										7
33.0	19	2													2
33.5	13		1					1							2
34.0	2														
34.5	1														
35.0	1		1												1
35.5	1														
36.0	7	2													2
36.5	8														
37.0	10														
37.5	12														
38.0	9														
38.5	2														
39.0	6	1													1
39.5	1														
40.0	3														
41.0	2														
44.5	1														
45.0	1														
45.5	1														
47.5	1														
49.5	2														
50.0	1														
Not measured	1				1										1
Total	1,000	60	30	15	7	4	1	1	2	2	1	2	2	2	129

[1] 101 days. [2] 359 days.

EXPERIMENT No. 7

Thinking that the attachment of tags to the rapidly moving caudal region of the mackerel was less desirable than to the less active forward parts, a modification of the strap tag was devised for attaching to the operculum. Higgins had found (unpublished notes) that No. 3 strap tags on the operculum of the mullet, *Mugil cephalus*, caused enlargement of the perforation made by the clinching point, presumably by rotation of the tag around its point of attachment. He suspected that the enlargement proceeded until it reached the margin of the operculum thus allowing the tag to drop off. This modified tag was three times as broad as the standard tag and had two clinching points to prevent rotation. In September 1926, tags of this type were attached to 396 individuals caught by purse seines with the same procedure as in experiment 5. No returns resulted and although this might have been owing to the rough treatment inevitable with purse-seine-caught mackerel, it is more likely that the lack of returns was due to loss of tags from the operculum, for 20 bull's-eye mackerel, *Pneumatophorus grex*, marked with this style of tag and held in a livecar at Woods Hole lost their tags within 14 days. The loss appeared due to necrosis of the tissue.

INFLUENCE OF TAGGING ON THE MORTALITY OF MACKEREL

The diminution in returns of the mackerel released in experiments 2 and 6 during the first month after release is of interest in providing field evidence on the merits of the methods used in tagging mackerel in 1925 and 1927. In experiment 2 (table 26) the returns from mackerel released during June 23 to July 3 diminished at an average rate of 54 percent per 5 days during the first three successive 5-day periods. The returns from those released during subsequent periods in the same experiment diminished at an even higher rate.[2] In experiment 6 (table 27) the returns declined at a nearly uniform rate of 50 percent in the first four successive 5-day periods. Such declines might be due to (1) the early loss of tags from the fish; (2) rapid dispersal of the fish from the point of release to areas in which less fishing was done; (3) early mortality of the fish tagged.

That some tags were lost from the mackerel is probable. In tables 28 and 29 are given the returns of fish by size groups, demonstrating that the maximum returns of the mackerel tagged in 1925 were of the 14- to 15-inch size groups, and of those tagged in 1927, the best returns were of the 30.5 to 32.0 centimeters (12 to 12½ inches). In each case the tags were chosen of a size to fit the prevailing size of mackerel and it is seen that the maximum returns in each case were close to modal length of the mackerel released. Below these sizes the returns were appreciably poorer, and we consider it probable that a portion of the tags placed on the smaller mackerel slipped off over the caudal fin. If the percentage returns from the groups of maximum return are indicative of the returns to be expected when there is no loss of tags, the loss of tags from mackerel 8 to 12 inches may be estimated at 60 percent, and the loss from mackerel 12½ to 13½ inches, at 36 percent in

[2] This higher rate may reflect the care with which the mackerel were handled. Those tagged during June 23 to July 3 were under the immediate supervision of a trained biologist. Subsequent to that date the tagging was done by an untrained crew, without immediate supervision.

TABLE 28.—*Relation between size of mackerel tagged and percentage of returns in 3 groups of mackerel tagged at Provincetown, Mass., 1925*

Length, inches[1]	June 23–July 3			July 9–22[2]			July 29–Aug. 5			Total		
	Released	Recaptured		Released	Recaptured		Released	Recaptured		Released	Recaptured	
	Number	*Number*	*Percent*	*Number*	*Number*	*Percent*	*Number*	*Number*	*Percent*	*Number*	*Number*	*Percent*
8	1									1		
8½				1						1		
9	4			4						8		
9½	5			22			1			28		
10	4			108	3		12			124	3	
10½	3			114	5		37	3		154	8	
11	4			112	6		45	1		161	7	
11½	14	1		40	2		51	2		105	5	
12	21	1		35	4		37	2		93	7	
Total	56	2	3.6	436	20	4.6	183	8	4.4	675	30	4.4
12½	15			39			47	4		101	4	
13	56	2		49	5		67	4		172	11	
13½	197	15		96	11		175	9		468	35	
Total	268	17	6.4	184	16	8.7	289	17	5.9	741	50	6.7
14	378	31	8.2	199	24	12.1	303	24	7.9	880	79	9.0
14½	138	21		98	10		186	21		422	52	
15	39	6		49	3		24	3		112	12	
Total	177	27	15.2	147	13	8.8	210	24	11.4	534	64	12.0
15½	8			19	2		6	1		33	3	
16	14			23	3		3			40	3	
16½	11			2			1			14		
17	8			11	2					19	2	
17½	8	2		1			1			10	2	
18	8			6						14		
18½	3			3						6		
19	5			3						8		
19½	3									3		
20	1			2						3		
21	1									1		
Total	70	2	2.9	70	7	10.0	11	1	9.1	151	10	6.6
Grand total	949	79	8.3	1,036	80	7.7	996	74	7.4	2,981	233	7.8

[1] Measurements were made to the nearest quarter-inch, but there was such marked bias in favor of the whole-inch and half-inch intervals that the quarter-inch measurements were grouped with the preceding whole-inch group and the three-quarter-inch mark with the preceding half-inch group, so that the mid points of the class intervals in this column are 8⅛, 8⅝, 9⅛, 9⅝, etc.

[2] Exclusive of the last 258 mackerel tagged on July 22, omitted because suspected of being in exceedingly poor condition when released.

TABLE 29.—*Relation between size and percentage of returns from 1,000 mackerel tagged and released at Woods Hole, July 15–27, 1927*

(EXPERIMENT NO. 6)

Length, centimeters	Number tagged	Number returned	Percent
25.5–28.5	104	8	7.7
29.0–29.5	194	21	10.8
30.0	158	20	12.7
30.5	138	22	15.9
31.0	117	22	18.8
31.5–32.0	148	20	13.5
32.5–34.5	72	11	15.3
35.0–50.0	69	4	5.8
Total	1,000	128	12.8

experiment 2. Similarly, in experiment 7, the loss of tags from the group 25.5 to 28.5 centimeters long, may be estimated at 51 percent and the loss from the group 29.0 to 30.0 centimeters at 27 percent. If only the size groups of maximum return be considered, the rate of diminution in both the 1925 and 1927 experiments is still about 50 percent per 5-day period during the first 15 or 20 days, indicating that the loss of tags, although affecting total returns of small mackerel, was distributed uniformly during the three or four 5-day periods immediately after release, and hence was not responsible for the rate of diminution of returns.

It is probable also that the rapid diminution of returns from these experiments in part was due to the dispersal of mackerel from the point of release to areas less intensely fished. In both experiments tagging was done at pound nets, and even slight travel of the tagged fish in an offshore direction would take them out of reach of the gear alongshore. However, it would also bring them into the range of the purse-seine fishery. This is particularly true of those released in Provincetown. So also, movement along the shore would take them into the range of pound nets elsewhere. Inasmuch as the returns from distant points were negligible, it does not seem that the rapid diminution was due to dispersal. On the contrary, it appears more likely that the population of tagged fish of these particular experiments stayed more or less in the vicinity of their release during the remainder of the summer. By contrast, a tagging experiment done at Woods Hole, Mass., June 8–17, 1925 (table 25), affords an example of the results obtained when there is rapid dispersal. Of the returns during the first month after release, 50 percent, rather than a negligible number, came from distant points.[3] All things considered it would appear that only a part of the diminution of the early returns in experiments 2 and 7 was due to scatter of the fish, the remainder, perhaps the major portion, resulted from other causes.

Principal among the other causes is quite plainly the mortality of the mackerel during the first 2 weeks after tagging. Experiments on holding mackerel in confinement have shown that they are subject to high initial mortality as the result of catching and handling. In two experiments the loss was 36 and 70 percent and this is thought to have taken place during the first 2 weeks after catching. A 50-percent mortality per 5-day period would be the equivalent of 75 percent in 15 days. So it appears that the rate of decline in number of returns from field releases was not far different from the mortality in holding experiments. The number of holding experiments was too few to establish a reliable average-mortality expectancy, but perhaps adequate to demonstrate that the bulk of the decline in returns must have been due to mortality and only a minor part to dispersal of mackerel from tagging points.

TESTS OF THE SUITABILITY OF VARIOUS TAGS FOR MARKING MACKEREL

Thus, the foregoing experiments yielded returns that either were scanty, or fell sharply during the first few days, owing to loss of tags and to mortality of the tagged fish. It was also observed that (1) the caudal peduncles of some of the banded mackerel that were recaptured were sore; (2) some of the specimens were in an emaciated condition; and (3) a dead, banded mackerel was found stranded on the beach in the vicinity of its release 3 days after tagging. Therefore, field operations in tagging were suspended pending improvement of tagging technique.

Up to this time no means had been found to keep mackerel alive in confinement for more than a few days. In 1929, Hall (1930) in the course of studying respiration of the mackerel was led to the conclusion that this species could be held in confinement if provided sufficient space to swim about more freely

[3] This rapid scatter to other points should have caused a rate of diminution in local returns even greater than those of experiments 2 and 7. Unfortunately, the local returns were too few to be significant. There were three, two, and one returned locally in the first, second, and third successive 5-day periods after tagging, respectively. Presumably these low returns were due to the rapid departure of the mackerel from the region.

than in the relatively small aquaria customarily used for other marine species. The outdoor pool at the United States Fisheries Biological Station at Woods Hole, Mass., provided the space needed. Its dimensions, 24 feet wide, 89 feet long, and 3 to 7½ feet deep, and its tidal circulation through four openings totaling 29 square feet (providing an exchange of one-sixth to three-quarters of the water at minimum and maximum tides, respectively) proved adequate for holding mackerel alive and in good condition during the summer and autumn months.

About 70 tinker mackerel were brought from a local pound net in the live well of a small boat and placed in this pool on June 26. During the subsequent week many of these showed effects of injuries probably received while being handled and transported, for they developed conspicuous white patches, usually on the snout, tail, and sometimes on the sides of the body. After a week or 10 days, these evidences of injury disappeared, in part through healing, and in part through death of the injured individuals. From this time on, the mackerel ate eagerly of the ground fish and squid provided daily.

On July 22, 26 days after the mackerel had been placed in the pool, the 45 survivors were marked with 2 styles of ring tags.

On July 24 and 26, 184 additional mackerel, brought from local pound nets by means of a live car, were placed in the pool with the tagged individuals. Within 3 days the newly added individuals developed sores principally on the sides of the body, and during the first week 28 dead or dying mackerel were removed from the pool. Additional carcasses were noted on the bottom. In the meantime, the tagged mackerel continued to feed as formerly and appeared not to be injured by the tagging operation. By July 31, evidences of sores had disappeared from the mackerel of the new stock and they were feeding as readily as the original stock.

On August 22, when all mackerel were removed from the pool, there were 31 survivors of the tagged fish and 55 survivors of the stock that had been added on July 24 and 26. Those with tags were returned to the pool. Of those without tags, most were marked with additional styles of tags and returned, and a few were returned without tagging, to serve as controls.

On October 24, the experiment was ended by seining out the survivors. Only 18 were found. If none eluded the seining operation, this shows a mortality of 84 percent.

Since the mortality was not due to the tags (for controls suffered mortality equal to that of the tagged fish), to lack of nourishment (the survivors were fat and plump at the end of the experiment), or to unfavorable temperatures (varying between 68° and 72° F. between July and the first half of September, temperature declined gradually to 59° F. by October 23, hence was well within the range known to be tolerated by unconfined mackerel), I am inclined to ascribe it to the effects of the heavy rains of September 17 which flooded the harbor with muddy water which persisted for 3 days and must have lowered the salinity appreciably. The turbidity of the water precluded direct observation of the condition of the fish, but a sharp reduction at this time in the readiness with which food was accepted, indicated a significant change in the condition of the fish.

Despite the few survivors at the end of the experiment, certain of the results appear significant when growth rate and mortality of the individuals marked with the different styles of tags are compared with controls.

The various styles of tags with the names used to designate them are illustrated in figure 21. The dimensions were as follows:

Celluloid band: Made of celluloid strips 0.025 inch thick, 5/16 inch wide and 2 inches long (0.635 by 8 by 50 millimeters) molded to form a circle 7/16 inch (11.1 millimeters) in inside diameter, with an overlap of about ⅛ the circumference.

Celluloid ring: Made of rods of celluloid 3/32 inch (2.5 millimeters) in diameter and 1½ inches (38 millimeters) long, cut obliquely at the ends to fit together when molded to a circle of ⅜ inch (9.5 millimeters) inside diameter.

Rubber band: Drainage tubing ⅜ inch (9.5 millimeters) in diameter with walls 0.013 inch (0.33 millimeter) thick, cut into sections to provide bands ⅜ inch (9.5 millimeters) wide.

Internal tag: Strip of celluloid 0.025 by 5/16 by 1½ inches (0.635 by 8 by 32 millimeters) rounded at the ends.

Each of these was chosen for particular reasons. The celluloid band was included to test our conclusions as to the earlier taggings with the celluloid poultry band. It was similar to the latter, except

that it was of thinner stock and of a smaller size appropriate to the smaller mackerel on which it was to be placed.[4] The celluloid rings were included, at the suggestion of Henry B. Bigelow, to see whether the smoothly rounded form would be less injurious than the sharp-cornered bands. The rubber bands were selected to see whether a soft material would be less harmful than the hard celluloid, and the internal tags were tried because of their superiority over external tags demonstrated on other species by Nesbit (1933).

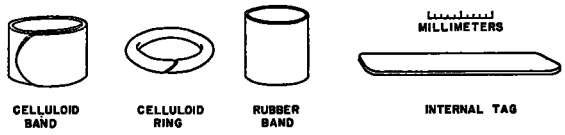

FIGURE 21.—Diagrams of tags tested in holding experiments.

In the marking of July 22 when two styles, celluloid bands and celluloid rings, were applied to the mackerel, the mackerel were tagged alternately with the bands and rings in the order that they were dipped up from the net pocket. In the marking of August 22, the mackerel were again handled in the order dipped from the pocket. Those already tagged the month before were measured and released, while the ones not bearing tags were treated in three different ways. All 27 centimeters long were tagged with rubber bands; all 27.5 centimeters long were released as controls; and the remaining sizes were marked by the insertion of internal tags. The selection of a particular size for rubber bands and controls was necessitated by their lack of individual identifying marks which required that the fish of each lot be of the same size at the time of release if their subsequent growth was to be determined.

All measurements were made to the nearest half centimeter on the measuring board described in appendix A. In table 30 the lengths are given in half centimeters just as they were originally entered in the records, but elsewhere they are given in centimeters, or decimal fractions thereof.

In table 30 are given the records of those fish that bore numbered or lettered marks. The records on the mackerel not bearing numbered marks are as follows: Of the 15 mackerel, each 27.0 centimeters long when marked with rubber bands on August 22, only 1 was found on October 24. It measured 27.5 centimeters, a gain of 0.5 centimeter since tagging. Of the 16 controls, each 27.5 centimeters long at

[4] The even-numbered tags of this style had the interior corners beveled, the odd-numbered ones had "square" corners. Since we could discern no significant differences in the results with the beveled and unbeveled rings (table 29) they have not been treated separately.

TABLE 30.—*Records of experiments with celluloid bands, celluloid rings, and internal tags*

[Lengths and increments are given in half centimeters. To convert to centimeters divide by 2]

Celluloid rings						Celluloid bands				Internal tags			
Serial letter	Length			Increment		Serial No.	Length		Increment	Serial No.	Length		Increment
	July 22 [1]	Aug. 22	Oct. 24	July 22–Aug. 22	Aug. 22–Oct. 24		July 22 [1]	Aug. 22	July 22–Aug. 22		Aug. 22 [1]	Oct. 24	Aug. 22–Oct. 24
A	48	51		3		69	47			43	56		
B	54	57	61	3	4	70	49			44	56		
C	52	56	61	4	5	71	49	52	3	46	53	62	9
D	52	57	64	5	7	72	51	53	2	47	52		
E	52	55		3		73	49	(2)		48	53		
F	52					74	50			49	57	64	7
G	50					75	50			50	56		
H	51	53	59	2	6	76	52	54	2	52	53		
I	51	55	60	4	5	77	51			53	51		
J	48	51	55	3		78	47	50	3	54	56		
K	52	56	62	4	6	79	50	54	4	55	56		
L	51	54		3		80	52	53	1	56	57		
M	52	55		3		81	49			57	52	61	9
N	51	57		6		82	51	52	1	58	53	60	7
O	47	48		1		83	49	51	2	59	53		
P	50	53		3		84	51			60	57		
Q	51	54		3		85	47			61	56		
R	50	55		5		86	48	51	3	62	51		
S	51	54	62	3	8	87	49			63	52		
T	53	55		2		88	49			64	52		
U	44	47		3		89	49	50	1	65	53		
V	54	56		2		90	52			66	53		
W	50	53		3						67	51		
										68	53	58	5

[1] Tags were applied on this date.
[2] Tag was found in skiff from which tagging was done Aug. 22, evidently having slipped from the mackerel unobserved.

the time of release, August 22, four survived the experiment and were 30, 31.5, 31.5, and 32 centimeters long, respectively, an average growth increment of 3.75 centimeters during the period August 22 to October 24.

Examination of the relation of size to mortality and growth increments gave very little evidence that the size of the mackerel was correlated with its subsequent fate except in the case of the 22 mackerel marked with celluloid rings. The survivors (to October 24) of this lot were all from the upper half of the range of sizes at time of tagging. However, the numbers involved were so few that the significance of this is questionable.

Considering, first, the period of August 22 to October 24 for which there are available comparisons between all four styles of marks and the controls, it is evident that there were large differences in the rates of survival and of growth of the mackerel in various experiments (table 30). The mackerel with internal tags compare most favorably with the controls, having an average growth rate practically identical with that of the controls, and a survival rate that was not significantly different from that of the controls. The celluloid rings appeared not to have affected the survival of the mackerel but to have caused a definitely lower growth rate, their average increment of 3.0 centimeters being 21 percent less than the increment of 3.7 centimeters registered by the controls. The celluloid bands and rubber bands appear to have had markedly adverse effects on the mackerel, causing almost complete mortality and, judging by the lone survivor bearing a rubber band, this style of mark caused a 60 percent lower growth rate than was experienced by the controls. The lack of survivors among the celluloid-banded mackerel during the period August 22 to October 24 precludes comparing growth with that of the controls; but the mackerel marked with celluloid bands and celluloid rings during the period of July 22 to August 22 had an average growth of 1.0 centimeter and 1.6 centimeters respectively. If we may assume that the last-named increment (1.6 centimeters) was 20 percent less than would have been registered by untagged fish, then the growth of the celluloid-banded fish was reduced by about 50 percent, a figure not unlike that of the rubber-banded mackerel. Thus it appears that bands, either of celluloid or of rubber, caused almost complete mortality of tinker mackerel within a few months; that celluloid rings did not greatly affect the survival of mackerel, at least during a 3-month period, but caused some slackening of growth; and that internal tags produced no discernible effect, either on growth or on mortality.

In the case of the celluloid bands, it is evident that the mortality data cannot be taken at their face value due to loss of tags from the fish. Although designed to fit loosely so as not to exert pressure on tissues, yet closely enough to be held in place by the flaring lobes of the tail fin, some of these tags must have been slightly too large, for one was seen to slip off over the tail fin shortly after tagging; another was seen to slip off 5 days later while the mackerel were being fed; and a third came off while the mackerel were reexamined August 22, for it was found in the bottom of the skiff shortly after conclusion of the work on that day. Hence, it would appear that the 45.5 percent so-called "survival" during the period July 22 to August 22 must be a minimum, for it is known that at least three tags were lost in this period and it is probable that additional ones were lost unobserved. It is possible that almost the entire diminution in number of banded mackerel may have been due to loss of tags rather than to mortality.

TABLE 31.—*Survival and growth of mackerel marked by various means during summer of 1933*

Marks used	July 22	Aug. 22	Survived from July 22 to Aug. 22 [1]	Average growth of survivors July 22 to Aug. 22	Oct. 24	Survived from Aug. 22 to Oct. 24	Average growth of survivors Aug. 22 to Oct. 24
	Number	*Number*	*Percent*	*Centimeter*	*Number*	*Percent*	*Centimeter*
Celluloid bands	[2] 22	10	45.5	1.1	(3)	----------	----------
Celluloid rings	[2] 23	21	91.4	1.6	7	33.3	3.0
Rubber bands	----------	[2] 15	----------	----------	1	6.7	1.5
Internal tags	----------	[2] 24	----------	----------	5	20.8	3.7
Controls	----------	[4] 16	----------	----------	4	25.0	3.8

[1] The numbers in this column includes only those survivors that retained the marks. It is known that at least some of those marked with celluloid bands lost the band soon after tagging, but they could not be distinguished from the unmarked mackerel that were present in the pool on the date of reexamination.
[2] Tagged this date.
[3] None survived except 1 doubtfully identified with this experiment by means of scar around caudal peduncle.
[4] Released this date.

On the other hand, there are three reasons for believing that the subsequent losses (i. e., after August 22) of celluloid-banded mackerel must have been due mainly to mortality: (1) All that were loose fitting enough to come off had opportunity to do so during the first month; (2) all that stayed on during the first month would be far less likely to be lost later, for the mackerel, by that time, had grown so that bands would fit more closely; (3) during the first month the bands caused sufficient soreness of the tissues to leave scars that could be detected at the last examination. Only one such scarred mackerel was found, so there cannot have been other survivors; and the final mortality in this experiment may be taken as 90 percent or 100 percent depending on whether this scarred individual should be counted. Since the loss of the tag presumably increased its chances of survival, this individual hardly can be regarded as evidence of survival of mackerel marked in this manner, and it may be concluded that this style of tag caused an unknown, but perhaps substantial, mortality during the first month after tagging, and complete mortality during the next 2 months.

The rubber bands gave similarly poor results. Of the 15 mackerel tagged on August 22 only 1 survived to October 24. In this case it is certain that the loss was due to death rather than to the loss of tags, for the rubber bands were too tight rather than too loose. Although the mackerel, by actual measurement, had caudal peduncles ⅜-inch in diameter at the slenderest point, and the diameter of the band also was ⅜-inch, the width of the band was such as to cause it to extend anteriorly and posteriorly of the slenderest part of the caudal peduncle, thereby causing slight pressure at the anterior and posterior edges of the band. This evidently was sufficient to cause necrosis of the underlying tissue, for both the survior mentioned above, and another that died 5 days after tagging, lacked skin on the area underneath the band which seemed to have "eaten" down the tissue in a sharply defined band around the caudal peduncle.

It is doubtful whether an improvement might be gained by using more loosely fitting rubber bands, for only a slight enlargement of the band would allow it to slip over the tail fin. Rubber bands are flexible enough to conform to the cross-sectional shape of the tail fin and thus slip off more easily than the stiffer celluloid band of the same diameter. Hence, it appears that rubber bands are unsuitable. Furthermore, the mere fact, established by these experiments, that bands must fit the caudal peduncle neither too loosely nor too tightly, renders this style of tag impractical for general use in field experiments where the variation in size of fish would require an extensive range of sizes of bands and an accurate judgment of size to apply.

The celluloid rings were intermediate between the bands and the internal tags in their effects on the mackerel. They apparently did not cause mortality but did retard the growth rate. It cannot be assumed, however, that the mortality of mackerel bearing the rings would remain unaffected over longer periods of time. At the end of the 93-day period, all mackerel marked with rings had sores encircling the caudal peduncle where the rings, although loose, came into contact with the peduncle during the lateral vibrations of the caudal region while swimming. These sores appeared as intense as the ones found August 22 on the mackerel that had carried celluloid bands during the previous month; that is, the skin was in most cases entirely absent from the sore region, leaving the flesh and sinews exposed. Though there was no active bleeding, the sores were decidedly reddish. The only generally apparent difference between the sores caused by the rings and those caused by the bands was the greater area involved and the deeper notching of the caudal lobes by the bands. That the rings as well as the bands caused soreness was surprising, for it was anticipated that their smoothly rounded surfaces could not chafe the skin as readily as the sharp corners of the bands. This makes it seem that soreness is caused by contact or impact as well as by chafing. If it may be assumed that the disturbance of internal salt-balance is one of the important effects of sore areas on the protective tissues of the fish, it is not surprising that the celluloid rings should have affected mackerel less than the celluloid bands, for the area of soreness was much smaller in the case of rings than of bands.

Inasmuch as the soreness caused by celluloid rings persisted throughout the experiment, showing no evidence of healing, considerable doubt is cast on the retention of the tags or the survival of the fish much beyond the length of time demonstrated by the experiment. Enlargement of the caudal peduncle through growth and the resultant increased pressure can be expected to lead to eventual impairment of the caudal fin as an organ of propulsion and ultimate destruction of the fish, either through impairment of

feeding or inability to escape from predators. Hence, this tag can be considered of use during only a few months when applied to young, rapidly growing fish and possibly as much as several seasons on old and slowly growing ones.

In marked contrast to the results obtained with the bands and rings, the internal tags appeared to have had no adverse effects. Not only do the records of mortality and growth rate (table 31) indicate this, but examination of the mackerel at the close of the experiment revealed no harmful effects. In all cases the incision through which the celluloid strips had been inserted, had healed, leaving only a faint scar. In all cases save one, the tag lay alongside the internal organs or partly hidden by them. No adhesions or inflamed areas were evident. In the one exception, the tag had not entered the body cavity but had lodged under the peritoneal lining of the body wall. In this position it had caused no apparent soreness of tissues with which it came into contact. Evidently this method of marking is ideal in its lack of effects on the mackerel and there is no reason to doubt its permanence.

An important objection to the internal tag is that usually it will not be found by the person who can furnish information as to the date and locality of capture, for mackerel pass from fishermen to wholesaler to retail dealer without being gutted, except for a small fraction of the catch which is salted or canned. To some extent this difficulty may be overcome by printing on the tag instructions for ascertaining the source of tagged fish bought from dealers. Whether a percentage sufficiently high to be useful can be traced to their source remains to be demonstrated. If not, marking experiments should be of two kinds: (1) The internal tag for quantitative results; (2) an external tag for short-time, qualitative results. For external marking, the celluloid ring (or some better one yet to be devised), is indicated.

In addition to demonstrating the effects on the mackerel of the several types of tags, these tests incidentally call attention to a feature of tagging operations not previously appreciated. This is the high initial mortality attending the catching and transfering of the experimental lots to impoundment. The first lot suffered 36 percent and the second lot 70 percent mortality during the first two weeks after capture. This initial mortality might have resulted from confinement of the fish, but in view of the subsequent good condition of the impounded mackerel, we are more inclined to believe it was due to the catching operations. If this is correct, mackerel tagged and released directly after catching would be subject to a high and variable initial mortality. This would need be considered in treating results quantitatively.

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ON THE EFFECTIVENESS OF SPERMATOZOA OF THE PINK SALMON (*ONCORHYNCHUS GORBUSCHA*) AT VARYING DISTANCES FROM POINT OF DISPERSAL

By RICHARD F. SHUMAN, *Aquatic Biologist*

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INTRODUCTION

The suggestion often has been made that, in the natural spawning of salmon, the ratio of males to females in the escapement need not even approximate 1 : 1; that a relatively few males can achieve successful and efficient fertilization of the eggs of a great many females. This could be accomplished in only one of, or a combination of, two ways: (1) By each male giving service to two or more females, fertilizing the eggs of each in turn, or (2) by the spermatozoa of spawning males being disseminated throughout the stream waters in such a manner that the eggs of all females in the stream will be fertilized, even though each female does not have a male in attendance during her spawning act.

It is unlikely that dual or multiple service by one male played any significant part in the perpetuation of virgin salmon populations, since existing data indicate that, on the average, the two sexes are produced in approximately equal numbers; with no imposed selectivity in mortality rates the sexes would have remained fairly equal in numbers, and there would have been little reason or opportunity for one male to give service to more than one female. With present-day fishing intensities and low-population levels, the sex ratio may vary from year to year in any stream, but seldom (if ever) is the effect of selective fishing accurately measured, and there is a reasonable doubt that the natural production of the sexes is as varied as may be indicated by weir counts or other methods of sampling within the river systems. Foerster (1931: 123) stated, "A shortage of males would seem to represent either one of Nature's weaknesses or a faulty system of regulation of commercial fishing." It is probable that when there is a significant superiority in numbers of either sex in the escapement, the inequality is caused by selective fishing.

Rutter (1902 : 134), in a study of the quinnat (king) salmon of the Sacramento River, reported that there was no evidence that "one sex is produced more than the other." Barnaby (1944: 277) found that with the red salmon of the Karluk River, Kodiak Island, Alaska, the females predominated in the escapement each year from 1923 to 1933, on the average constituting 56.1 percent of the fish in the river. He recognized that the gill-net fishery a few miles from the river mouth was selective, taking more males than females, but he did not believe this factor accounted for the discrepancy in the sex ratio of salmon found in the river, and he offered no explanation for the phenomenon.

At McClinton Creek, a tributary to Masset Inlet, Queen Charlotte Islands, the pink salmon spawn only in even-numbered years. Pritchard (1939: 238), presented counts of the sex ratios obtained at the weir for the cycle years 1930–38. These varied, but the over-all average showed only a slight predominance of females, which constituted 50.6 percent of the escapements. The effect of the commercial fishery on the ratios was not discussed.

In a study of the chinook (king) salmon of the Willamette River, Mattson (1948: 24) found that at the egg-taking station on the McKenzie River, a tributary to the Willamette, 51.3 percent of the fish were females. There was no discussion of the possible effect of commercial fishing.

At the United States Fish and Wildlife Service biological station, Little Port Walter, Baranof Island, Alaska, upstream migration counts have been obtained each year since 1934. During those years the sex ratios varied annually at the Sashin Creek weir, with no over-all significant advantage by either sex. The largest escapements obtained there were in 1941 and 1942. In the former year,

the escapement was 84,304, of which 46.2 percent were males; the following year, the escapement increased to 92,085, with 55.4 percent being males. The average for the 2 years was 51.1 percent males. It was believed that the commercial fishery had little effect on the spawning migration, since the area immediately surrounding Little Port Walter was relatively free from fishing effort.

Regardless of the sex ratio which obtains on the spawning grounds, pairing or mating of the sexes almost always occurs, and observations made by the author have indicated that with the various species of salmon there is a definite tendency toward monogamy. This tendency has been noted with salmon which, because of peculiar markings, could be identified throughout their courtship, nest building, and spawning activities. In each case, at the termination of spawning the male appeared to be in such a spent physical condition as to be incapable of attending another female, and he was observed on or near the nest until his death, which occurred soon after spawning. In these cases, there appeared to be little differential in the mortality rates of the two sexes. While it is probable that a male occasionally will attend more than one female, either because of the early death of the first mate, or because he has been driven from her by a stronger and more pugnacious male, the effectiveness of multiplicity of service must be demonstrated conclusively before it can be considered an important factor in salmon propagation under natural conditions.

It is not to be assumed that the attendance of a member of the opposite sex is a stimulus necessary to spawning responses. Rutter (1902: 135) stated, "the presence of the other sex is not necessary to excite either to spawning efforts. I have seen the female spawning alone at Battle Creek fishery, and other persons have reported similar observations at other places. In September 1900, I saw a male spawning alone near Sims, the female having been killed by a sportsman in order to get trout bait. Like observations are reported by other persons." The author has observed both pink- and red-salmon females extruding eggs over a redd when no male was in attendance.

Eggs deposited by these lone females could be fertilized only by spermatozoa which drift down to them from males spawning farther upstream. Dissemination of spermatozoa does occur, and was noted by Schultz (1935: 74) in a study of the spawning habits of landlocked sockeye. He stated, "Milt was plainly visible near the conclusion of the spawning act, which lasted about 2 seconds. The milt formed a dense, small, white cloud about 3 inches wide and 4 inches long, which was carried downstream by the current." When intensive spawning is taking place in any stream, great numbers of spermatozoa must be carried downstream and disseminated by the current. The degree of fertilization of eggs deposited by unattended females will be established by the density of the population of spermatozoa, and by the length of time during which the individual cells retain their vitality.

Rutter (1902: 73) reported that spermatozoa of king salmon retained their vitality for from 3 to 5 minutes, although the fertilization achieved under laboratory conditions fell from 88 percent at 30 seconds, to 38 percent at 1 minute, and to 4 percent at 1.5 minutes. Gray (1920: 309) stated that with the spermatozoa of trout (species?) "the period of motility is extremely short, namely 1½–2½ minutes," and he further stated that this period of motility was shortened markedly when the spermatozoa were placed in water.

The union of the spermatozoa and ova must take place very quickly under natural spawning conditions, since the rate of fertilization with normal, paired spawning appears to be very high. Hobbs (1937), in a study of the quinnat salmon, brown and rainbow trout, found that not more than 3 percent of the eggs extruded by the female failed to lodge in the prepared redds, and that lack of fertilization within the redds did not exceed 3.3 percent. White (1930) studying the eastern brook trout (*S. fontinalis*) found that through natural spawning, up to 79 percent fertilization was attained, while in his study of the quinnat salmon, Rutter (1902) conducted a series of experiments and concluded that "these various experiments indicate a high percentage of fertilization, probably over 80 percent."

Whenever a significant number of females spawn unattended, the success of spawning will be affected unless fertilization by free-drifting spermatozoa is as efficient as that obtained with natural, paired spawning. In order to test the degree of fertilization attained by these disseminated spermatozoa, a series of experiments were begun at Little Port Walter in the fall of 1941. As a preliminary step, a standard hatchery trough was set up, and a supply of water introduced. During the experiments the temperatures of the trough water were the same, or nearly the same, as those existing in Sashin Creek. The

tests were begun on September 15, by which time 34,145 pink salmon had been counted through the weir, with most of these fish being engaged in nest-building or spawning activities. Since only 3,700 feet of the stream are available to the salmon, and the average width is somewhat less than 60 feet, this number of fish constituted a large and concentrated (about 1.4 fish per square yard) spawning population; conditions therefore appeared favorable for the tests.

EXPERIMENTS IN 1941

In the late afternoon of September 15, a number of pink salmon of each sex were obtained from the lower reaches of the stream. Only completely ripe fish were selected, and all were killed and bled immediately. The abdominal cavity of the females was opened with a short knife as the eggs were needed, and three screen trays were partly filled in turn. As each tray was laden with eggs, another tray was placed over the top as a lid, and the trays were submerged in the creek at a point above the influence of salt water, yet below the majority of spawning fish. Each tray was rotated slowly for 5 minutes in such a manner as to assure complete circulation of water through the egg mass. In this way any active spermatozoa in the waters would have had ample opportunity to come in contact with and fertilize the ova. After 5 minutes' exposure, each tray was placed immediately in the upper end of the trough and secured there. A second group of eggs, estimated to be equal in numbers to those used in the above trial, were fertilized by standard hatchery methods and placed in the lower end of the trough; these constituted the control.

By November 1 all viable eggs appeared to be eyed out, but the experiment was continued until November 25, at which time cold weather threatened to freeze the pipe line. The trays were removed, the eggs examined and counted. It was assumed that fertilization had not been attained with any of the eggs which had failed to eye out, or which had been removed as dead during the course of the experiment. The counts, calculated volumetrically, showed that originally there had been 102,300 eggs, divided almost equally between the test and control groups. By sample counts it was determined that in the control group a fertilization of 62.8 percent had been achieved. A detailed study of the eggs in the test group showed that none of the ova had been fertilized.

EXPERIMENTS IN 1942

While the 1941 tests were enlightening, they by no means were conclusive, and further tests were made in 1942. Standard wire hatchery baskets were obtained, and two troughs were set up several days before the tests were to begin; the water supply and method of introduction were the same as those used the preceding year. This experiment was begun on the afternoon of September 12, a cloudy day, with the air temperature at 53° F. Although the level of the creek had been raised slightly by rains the preceding night, the water was not perceptibly discolored; conditions were normal. The temperature of the creek water was 55° F., while that in the troughs was 53° F.

A characteristic section of the stream was chosen for the first group of 1942 tests, near the place at which the work had been done in 1941. The water here was approximately 6 inches deep throughout; the bottom was composed of small and medium rubble. The current was moderate, with a velocity of 40 feet per minute.

At the upper end of the chosen section a marker stake was driven into the gravel, while downstream from it, alined with the current, five other stakes were driven at 1, 2, 4, 10, and 20 feet, respectively, from the marker stake. When this had been done, several ripe pink salmon, both males and females, were netted from the holding pool below the weir. The males were held in large buckets; the females were immediately killed, bled, and their eggs transferred to wire baskets. When enough eggs had been obtained for the first basket, four men, each carrying a ripe male salmon, stepped into the stream and began stripping or milking the fish so that the four streams of milt entered the water near to, and even with, the starting stake. A white cloud of milt was carried downstream and, although there was considerable lateral diffusion, the concentration of milt was such that the cloudiness of the water was distinct and dense at a distance of more than 50 feet.

Immediately this milking of male salmon had begun, the basket of eggs was immersed in the stream waters directly in the cloud of milt, the upper edge of the basket even with the 1-foot stake. The basket was rotated gently for a period of 3 minutes, during which time the flow of milt was maintained; spent male salmon were replaced as the necessity arose. At the end of 3 minutes the

eggs were washed in clear water and transferred to one of the hatchery troughs.

New fish were used for each of the succeeding tests, the performance being repeated at each of the remaining stakes, namely, 2, 4, 10, and 20 feet from the point at which the milt was ejected into the water. Later, one basket of eggs was fertilized by standard hatchery methods; this group constituted the control. The troughs then were covered with previously prepared lids.

Although the 1941 experiment had showed no fertilization among the eggs submerged in free-running creek water during the day, it was decided to repeat the tests in the dark of night. Since the extrusion of eggs and milt in natural spawning seldom is observed, it was thought possible that with pink salmon, spawning might take place principally at night, and that spermatozoa would be disseminated throughout the creek waters during the night hours, whereas none might be present in the daytime.

On the dark, cloudy night of September 22, the second group of 1942 tests was begun. Several ripe females were captured, killed, bled, and stripped into a wire basket at 10 p. m. The basket of eggs was submerged immediately into the creek waters at the usual working place. After 5 minutes of gentle rotation in the water, the basket was removed and placed in one of the hatchery troughs. A second group of eggs was treated in a like manner at midnight. At 10 p. m. the air temperature was 46° F., at midnight 44° F. From the former until the latter hour, the temperatures of both the stream and the trough waters remained constant at 53° F. At this time the stream level was normal, the waters clear. The weir count of pink salmon stood at 78,055, with most of these fish engaged in some phase of spawning activity, and well dispersed throughout the stream.

Standard hatchery procedures were followed in caring for the eggs during the course of the experiment, which was terminated on November 3 because of cold weather. The baskets were removed from the toughs, and counts of eggs in each basket determined volumetrically. As before, it was assumed that eggs which had failed to eye out, and eggs that died during the experiment never had been fertilized. All eggs were counted as fertilized when the eyespot could be seen, even though the larvae might be dead at the time of inspection. The number of fertile eggs in each basket was determined by actual count; the results are presented in table 1.

The attempt to achieve fertilization of ova by free-drifting spermatozoa (second group of tests) was completely unsuccessful; a detailed study of the eggs used in these tests yielded only negative results. The escapement was greater in 1942 than in the preceding year, and it is doubtful whether other pink-salmon streams in the Territory often reach the spawning-intensity which existed in Sashin Creek at either time. It, therefore, seems improbable that for this type of fertilization, more propitious conditions often (or ever) occur.

TABLE 1.—*Results of experiments made on pink salmon at Little Port Walter, Alaska, in 1942 to test the relationship between the effectiveness of spermatozoa and distance from point of dispersal*

Distance (in feet) of introduction of sperm to eggs	Number of eggs fertilized	Percentage of eggs fertilized	Number of eggs not fertilized	Percentage of eggs not fertilized
1	10,193	78.7	2,757	21.3
2	8,482	66.6	4,258	33.4
4	6,794	58.8	4,756	41.2
10	2,343	17.9	10,747	82.1
20	504	4.8	10,021	95.2
Control	9,822	86.4	1,553	13.6
Free-exposed, 10 p. m.	0	.0	13,510	100.0
Free-exposed, midnight	0	.0	14,350	100.0

It has been suggested that failure of fertilization by this free-exposure method might be the result of frightening the spawning fish while performing the necessary work in the stream. This is highly improbable. Observations made over a period of years have indicated that salmon engaged in spawning activities (whether actually spawning or nest-building) are not disturbed easily when approached quietly from downstream. These precautions were taken during the tests of both years, while in the night operations of 1942 no lights were used at or near the scene of activity. The females from which eggs were obtained were captured well away from the test location, and only one man entered the stream so as to minimize possible disturbance. In neither year was there any evidence of an interruption of the normal activities of nearby salmon.

Table 1 shows that a fertilization of 86.4 percent was achieved with the control group. The differential between this figure and the one obtained in the control group in 1941 is unexplained, but to the present discussion it is unimportant. Among the baskets of eggs exposed to spermatozoa artificially introduced to the stream waters (first group of tests), the rate of fertilization decreased from 78.8 percent at a distance of 1 foot, to 4.8 percent at a distance of 20 feet. The relationship of degree of fertilization

to time and distance is curvilinear, and is shown by the dotted line in figure 1, which is an exponential curve fitted by the method of least squares.

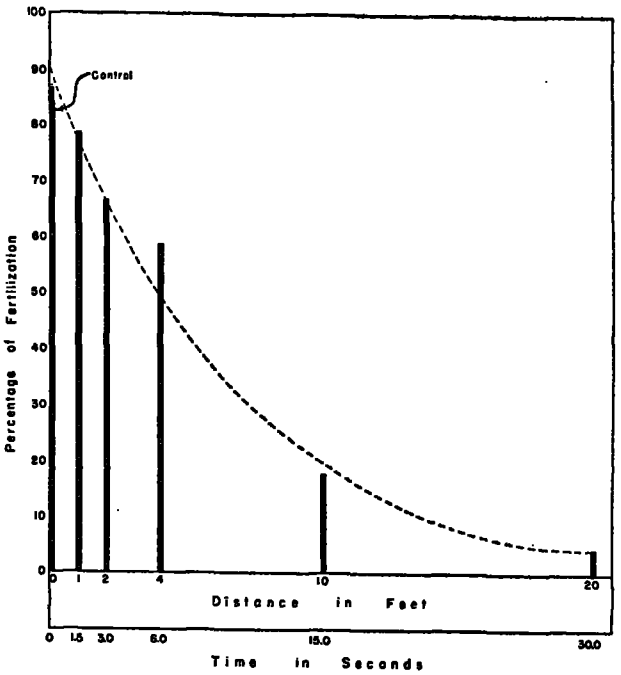

FIGURE 1.—The percentage of fertilization achieved in the various baskets is shown on the ordinate axis. On the axis of abscissa, O represents the point of dispersal of the spermatozoa, the distance to the baskets being designated in feet. Below is shown the number of seconds during which the spermatozoa were exposed to the water before coming in contact with the eggs in the baskets. The data from table 1 were used to produce the smoothed curve, dotted in the figure. The equation was: Log (percentage of fertilization) = 1.96 − 0.065 (distance in feet). The calculated standard error of estimate was 5.1 percent.

It is believed that the decrease in fertilization at the greater distances was caused not by dispersion of the spermatozoa but by their loss of vitality induced by extended exposure to the water. The lateral dispersion was considerable (the vertical dispersion having been limited by the shallowness of the water), but the density of the cloud of milt was such that even at 20 feet the eggs submerged in the basket almost were obscured from view. It is believed that many spermatozoa came into contact with each egg in the baskets, but that their vitality was so lowered that a union of the gametes was impossible. Certainly the density of the milt was greater at all distances than is found under natural conditions; no general cloudiness of the water from this source has been observed by the author or reported in the literature.

CONCLUSIONS

A consideration of the results obtained in these experiments makes it apparent that spermatozoa disseminated throughout the stream waters by spawning males will not achieve fertilization of eggs being deposited farther downstream, and that the eggs of lone-spawning females remain almost or completely unfertilized. For efficient fertilization of eggs each female must be attended by a male during her spawning acts. It remains to be demonstrated whether dual or multiple service by males can offset the difficulties imposed by the males being outnumbered greatly by the females. Until such demonstration, conclusively, can be made it will be advisable to regulate the fishery in such a manner that the ratio of males to females is approximately 1 : 1 in each spawning escapement.

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FLUCTUATIONS IN ABUNDANCE OF COLUMBIA RIVER CHINOOK SALMON (*ONCORHYNCHUS TSCHAWYTSCHA*) 1935-45

By Ralph P. Silliman

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FLUCTUATIONS IN ABUNDANCE OF COLUMBIA RIVER CHINOOK SALMON (*ONCORHYNCHUS TSCHAWYTSCHA*), 1935–45

By RALPH P. SILLIMAN, *Aquatic Biologist*

The United States Fish and Wildlife Service is charged by statute with the responsibility of reviewing plans for all water-use projects of the Federal Government, in order to determine their effect on populations of fish and to provide for the protection of these populations. Where runs of anadromous fish in the Columbia River Basin are concerned, the function has three primary aspects: (1) the determination of the species and size of the particular runs affected; (2) the ascertainment of the types of fish protective devices, if any, needed and the economic feasibility of these; and (3) the evaluation of the success of fish protective devices by comparison of the size of the runs before and after construction of dams and other such works. The present study is concerned with the most abundant of the Columbia River anadromous fish, the chinook (spring or king) salmon, *Oncorhynchus tschawytscha.*

In brief, the purposes of this report are to (1) present a detailed description of a method of calculating catch-per-unit-of-effort, for use in extending the present series of data both forward and backward; (2) indicate a method of deriving from the calculated catch-per-unit values a measure of abundance; and (3) make a preliminary appraisal of the importance of the various factors affecting abundance.

During the years in which the Fish and Wildlife Service and its predecessor the Bureau of Fisheries have carried on studies of Columbia River salmon, an enormous mass of statistical data on fish production has been accumulated, covering deliveries of 4 species of salmon and the steelhead trout to some 100 receiving stations along the commercial fishing zone of the river, and extending in time from 1897 through 1945. It is obvious that one worker (the author), with limited assistance, could gain useful information from such an accumulation of material only by limiting strictly the scope of the investigation. The study was, therefore, much restricted as to period covered, the area of the river included, the number of receiving stations within that area, the number of fishermen whose records were used, and the types of gear covered.

In relation to period of time, the most recent information is of course always of the greatest interest. The source data available in 1946 (when the study was started) ended with the 1940 fishing season; further original records were subsequently obtained bringing the series up to the most recent season for which the material was available, 1945. Calculations were carried backward as far as time available for calculations permitted—to the season of 1935.

As to area, the study was limited to deliveries made to those receiving stations of one large cannery which were located in statistical zone 1 (as established by the States of Washington and Oregon) of the commercial fishing area. This statistical zone (figure 1) includes the lowermost waters of the Columbia, opposite Pacific County, Wash., and contains the river's greatest concentration of fishing effort. It is subject to large tidal influence, and in reality is more of an estuary than a section of the river proper.

Gill nets (drift) constitute the most important form of gear on the Columbia; landings from this gear formed two-thirds of the total catch landed in the river during the decade 1935 through 1944. Because of the previously mentioned necessity for restricting the scope of the study, therefore, all calculations were based on gill-net data. Furthermore, the analysis was confined to the most consistent fishermen among the group delivering to the selected stations (this is explained in greater detail in the section, Selection of Fishermen, under the Computation of Catch-per-Unit-of-Effort).

The general effect of the above restrictions is to confine the study to a measure of the size of the runs of chinook salmon as they enter the Colum-

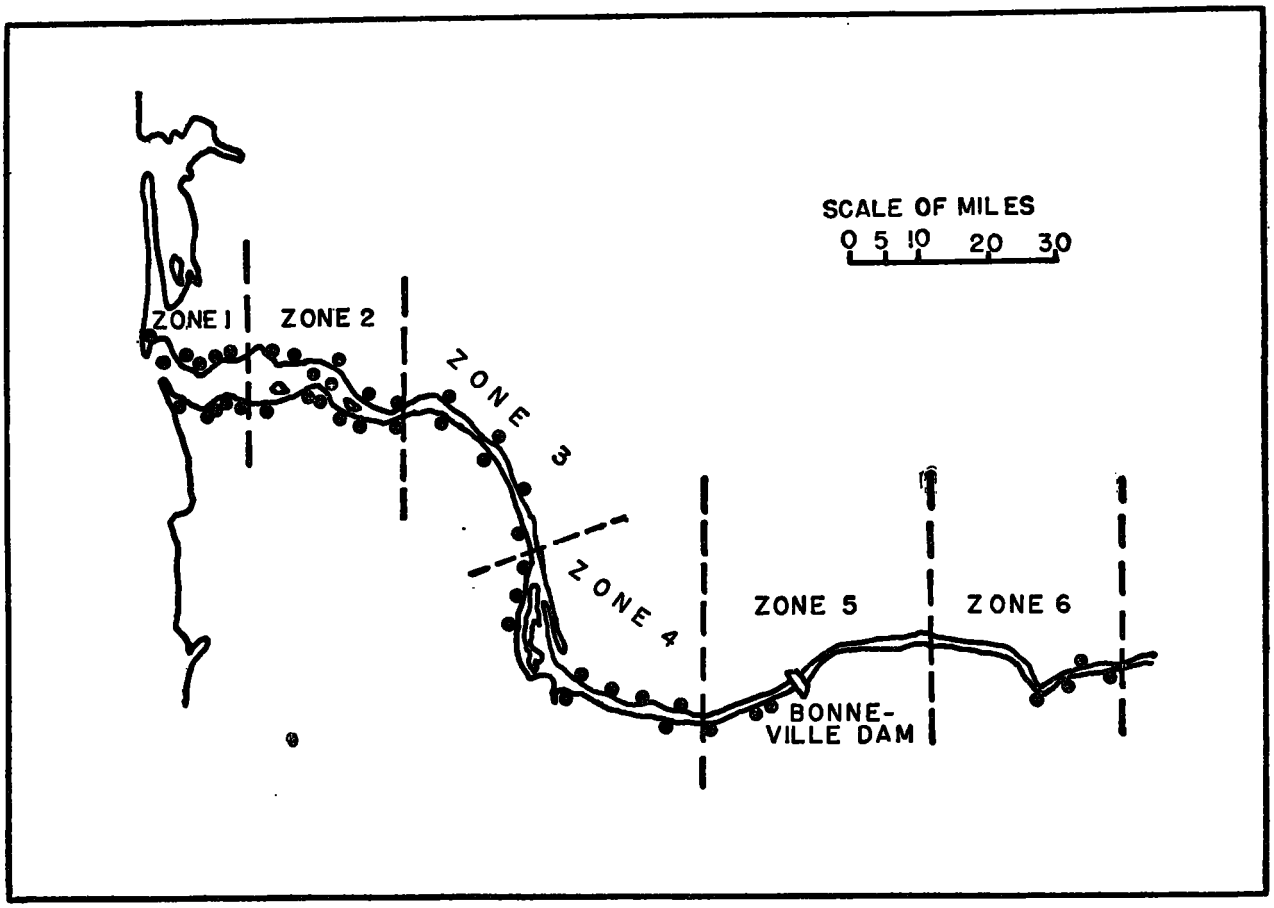

FIGURE 1.—Commercial fishing area of the Columbia River, statistical zones, and some fish-receiving stations (round dots).

bia River. It is important to recognize here that any effect of the currently (1949) large, ocean troll-fishery will have taken place before the measure occurs. This troll fishery is considered at length in another report (Silliman 1948), but it will suffice here to remark that in general its intensity seems to parallel that of the river fishery. To the extent that this seeming parallelism represents the true state of affairs, the river catch-per-unit will represent accurately the relative abundance of the runs as they enter the river, and it is relative abundance with which this study is chiefly concerned. The measurement of absolute abundance, of course, will require the addition to the river measurement of some estimate (such as that made in Silliman, loc. cit.) of the troll catch.

Many members of the Fish and Wildlife Service, both present and former, have helped me with this study. These include Harlan E. Johnson, John I. Hodges (now with the Oregon Fish Commission), Harold A. Gangmark, and Leonard A. Fulton, all of whom performed compilations and calculations; Floyd G. Bryant, who furnished information about the fishery; Mitchell G. Hanavan, who gave freely of advice on many phases of the biology of the salmon; and Elizabeth Vaughan, who counseled me on statistical matters.

I am grateful to the various canning companies on the Columbia River for their cooperation in making available to me the records of their operations, to the Fisheries Departments of Oregon and Washington for commercial catch data, and to William E. Ricker of Indiana University for review of the section on Estimation of Total Abundance.

COMPUTATION OF CATCH-PER-UNIT-OF-EFFORT

SOURCE DATA

Type of Record

The original records upon which the analysis was based consisted of cannery ledgers in which were entered the daily deliveries of individual gill-net fishermen. These fishermen (a more complete description of the gill-net fishery is given in Craig and Hacker 1940: 165, 182) operate gasoline-powered boats of characteristic type about 30 feet long. They set their nets alone or with one assistant, and are usually aided by a power-driven roller or net puller. The nets are of two types. Floater nets (used mostly near the mouth of the river) are simple walls of webbing constructed to float at the surface. Diver nets (the most efficient and popular form) are constructed to just touch the bottom, and usually are equipped with trammels of very large mesh through which the fish push the main net and get themselves caught in a bag. Both types are about 1,500 feet long and 20 feet deep, and are set at right angles to the direction of the current and allowed to drift with it.

Most of the fishing is done at night, the fisherman leaving in the evening (the exact time depending on the tidal stage) and returning in the morning to deliver his catch. Thus, each delivery record normally represents one night's fishing.

Selection of Season and Time Unit

Prior to 1943, fishing in the river was permitted the year-round except during March and April, and from August 25 to September 10. During the years 1943 through 1945, an additional closed period, May 20 to June 10, was in effect. In the trade the period from May 1 to August 25 is known as the spring season, and after September 10 as the fall season. Besides these closed seasons, there is a weekly closed period from 6 p. m. Saturday to 6 p. m. Sunday, during the spring season.

Most of the season's catch (95 percent for the period of this study) is landed during the months of May through September; in order to save time and to eliminate straggling season's-end catches, the analysis was limited to those 5 months.

Because of the Sunday closure during the spring season and because of a weekly cyclic fluctuation in the catches (Rich 1942: 128) it is desirable to subdivide the season into weekly time units. Rich (*loc. cit.*) has established a series of 7-day periods beginning with May 1, and this series will be used herein. The May–September fishing season contains 22 such periods (table 1), No. 22 ending on October 1 (the day October 1 has been included in all calculations in order to make the last period complete).

TABLE 1.—*List of 7-day periods used as time-units in the catch-per-unit-of-effort calculations*

Period No.	Dates included	Period No.	Dates included
1	May 1–May 7.	12	July 17–July 23.
2	May 8–May 14.	13	July 24–July 30.
3	May 15–May 21.	14	July 31–Aug. 6.
4	May 22–May 28.	15	Aug. 7–Aug. 13.
5	May 29–June 4.	16	Aug. 14–Aug. 20.
6	June 5–June 11.	17	Aug. 21–Aug. 27.
7	June 12–June 18.	18	Aug. 28–Sept. 3.
8	June 19–June 25.	19	Sept. 4–Sept. 10.
9	June 26–July 2.	20	Sept. 11–Sept. 17.
10	July 3–July 9.	21	Sept. 18–Sept. 24.
11	July 10–July 16.	22	Sept. 25–Oct. 1.

In contradistinction to the legal fishing seasons noted, certain large and obvious fluctuations in the catch during the fishing season have been recognized by fishery biologists and have led them to speak of at least three separate chinook-salmon runs. These are more readily apparent for data from early seasons, before certain of the runs were reduced in abundance, and can be seen in the graph of daily average gill-net catches delivered to one large cannery during the years 1926 through 1930 (fig. 2). Divisions have already been established (Rich 1942, table 13) between these, and are indicated on the graph.

The first mode or run apparently passes its peak into the river during the April closed season. Then, about the middle of June, a small peak occurs. Finally, there is the large run whose peak normally seems to occur during the August 25 to September 10 closed season. These three runs are ordinarily called "spring run," "summer run," and "fall run"; they will be so referred to herein. Incidentally, the May 20 to June 10 closed period referred to above was imposed to protect the spring run and summer run.

In the present analysis the following arbitrary divisions of the data have been made: spring run, weekly periods 1–4 (May 1 through May 28); summer run, periods 5–13 (May 29 through July 30); fall run, periods 14–22 (July 31 through October 1). The May 28 and July 30 division dates conform to those of Rich's (*loc. cit.*) table 12.

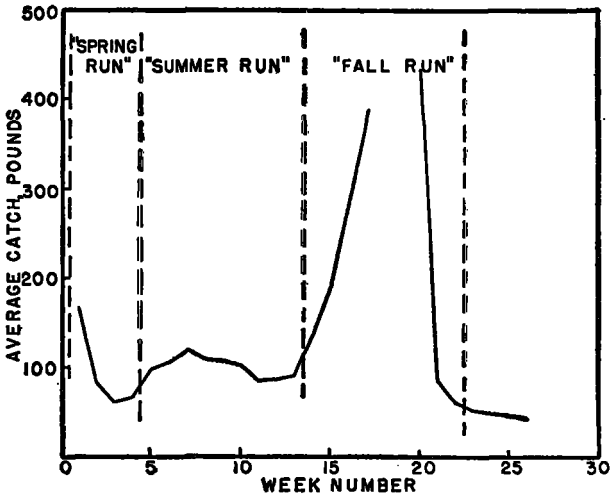

FIGURE 2.—Weekly average size of daily delivery of chinook salmon to a number of Columbia River receiving stations, 1926–30, by gill-net fishermen (for dates included in weekly periods (table 1)).

Selection of Fishermen

The aim in selecting fishermen whose records were to be used in the analysis was not to obtain a representative sample of the population of fishermen, but rather to choose fishermen whose catches would constitute a representative sample of the population of chinook salmon. Obviously, the most consistent fishermen would be most likely to obtain the best sample of the population (inconsistent fishermen tend to fish only during good fishing periods, and thus to oversample the most abundant parts of the run). The criterion of consistency was that a fisherman must have made, during each of a given pair of years, at least one landing during each month of the spring season or at least one landing during the fall season, and must not have made any landings outside of zone 1.

It is evident from the above that two groups of fishermen were selected, one for the spring season and the other for the fall. This was done purposely, since the fishery tends to change character between the two seasons. Many spring fishermen do not fish in the fall, and vice versa.

When the arbitrary criterion was applied to the available data, it was found that the number of fishermen so selected varied from 27 to 117 for the spring and from 30 to 92 for the fall season (table 2). In setting up the criterion the objective had been to keep the sample size between 30 and 100; a sample of 30 is considered the smallest to which large sample variability will apply, while 100 appeared to be a fully adequate sample size for the data used. Unfortunately, the number for the spring season of the 1944–45 comparison fell to 27, due to a change in the method of making entries in the cannery ledger. It was not deemed worthwhile, however, in view of the small size of the deficiency, to introduce nonuniformity by using a different criterion for 1944–45, or to change the criterion for the entire series of seasons to bring the sample size up for this one comparison.

TABLE 2.—*Numbers of fishermen selected by the arbitrary criterion of consistency (see p. 368 for explanation of criterion) and numbers whose records were used in the calculations*

Seasons compared [1]	Spring season		Fall season	
	Selected	Used	Selected	Used
1935–36	46	46	30	30
1936–37	117	97	55	46
1937–38	106	94	43	39
1938–39	85	85	45	45
1939–40	74	74	84	84
1940–41	55	55	68	68
1941–42	49	49	79	79
1942–43	48	48	92	92
1943–44	34	34	72	72
1944–45	27	27	66	66

[1] Method of comparison is described in the section, Use of Chain-Link Method.

As indicated in table 2, the sample size moved upward above 100 for the 1936–37 and 1937–38 spring comparisons. To save time in calculation, the number was reduced by discarding a sufficient number of fishermen at random to bring it below 100. In order not to disturb the natural relationship between spring and fall seasons, an equivalent proportion of the number of fishermen was discarded from the fall sample for the two comparisons. The actual sample sizes used are shown in table 2.

USE OF THE CHAIN-LINK METHOD

As indicated under Type of Record there are two major types of gill nets in use for catching chinook salmon in the lower Columbia River. There are innumerable variations of these, however, depending on the ideas and resources of the individual fishermen; boats also vary considerably as to size, power of engine, hull form, and equipment. Finally, fishing abilities, localities, and habits vary widely among the group of selected fishermen.

It is thus well-nigh impossible to set up a unit-of-effort of uniform and unvarying catching ability. However, since the attributes of a single fisherman tend to be relatively constant from one season to the next, it is possible to largely overcome the difficulty by comparing the performance of each fisherman in a given 7-day period of one season with his own performance in the corresponding 7-day period of an adjacent season. This is the method of chain linkage or link relatives familiar to economists; full descriptions are given in such statistical works as Croxton and Cowden (1943: 616).

ESTIMATION OF ZERO CATCHES

As mentioned above, the catch of a fisherman in a certain week of season *A* is compared in the present study with his catch during the corresponding week of season *B*. This is tantamount to calculating his catch per unit of effort for each of the two weeks, since it is implicitly assumed that the amount of effort expended is the same for both weeks. It seems reasonably safe to thus assume that, on the average, fishermen have put forth the same amount of effort during corresponding weeks of adjacent seasons, providing they made one or more catches during such weeks. There are not, however, any records of unsuccessful fishing trips, so that the data are not applicable to the situation where a fisherman made one or more catches during a certain week of one season, but did not make any catches during the corresponding week of an adjacent season. The question immediately arises, are such situations to be expected in significant numbers? In other words, is the number of zero catches great enough to be considered?

Examination of the frequency distributions of numbers of deliveries per week throws light on the above question. For instance, it is seen that during week 3 of the 1940 spring season (fig. 3), more than one-third of the fishermen who caught anything at all made only one delivery, with the occurrence of higher numbers of catches decreasing regularly as the number increases. Under such circumstances it seems practically certain that there were some fishermen who fished and caught nothing; it becomes necessary then to estimate the number of such cases. Such an estimation might be based on some assumed relation between the number of single and zero deliveries, but such a method would not be useful in connection with our method of comparing the adjacent-season performance of individual fishermen. We need to know not only how many fishermen fished during a given week, but which fishermen.

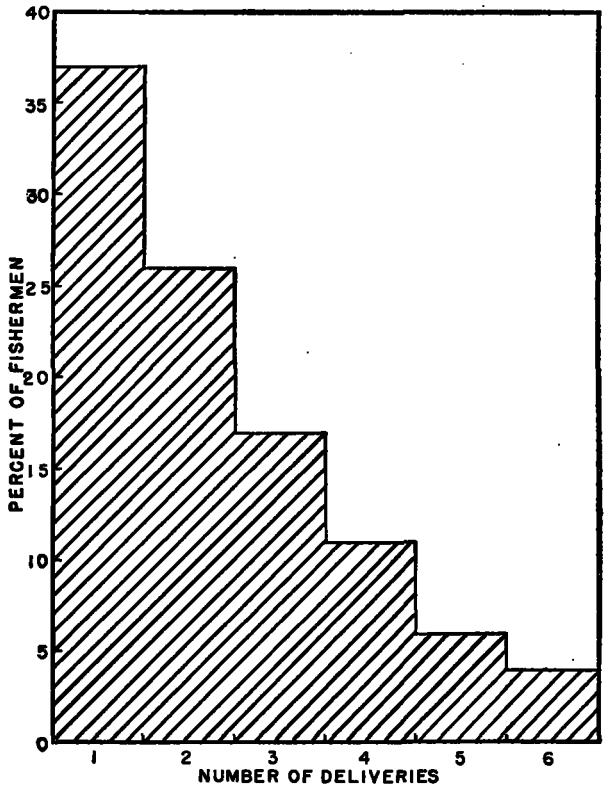

FIGURE 3.—Percentage distribution of numbers of deliveries of chinook salmon made by 54 Columbia River gill-net fishermen during week 3 (May 21–27) of the 1940 fishing season.

In setting up a rule for deciding which fishermen fished each week, a helpful assumption may be made. We may assume that it is extremely unlikely that any fisherman would fish as many as three successive weeks without a catch; under such circumstances he would probably drop out of the fishery until fishing conditions had improved. Taking this assumption as a basis we can list the weekly catches of all of the fishermen of the group considered and make the rule that a fisherman will be assumed to have been fishing during a given week even though he made no catches, if he made one or more deliveries during the preceding or succeeding week. To this we may add the requirement that at least 10 percent of the fishermen making deliveries during the week in question

have made only one delivery. This is based on the idea that if 90 percent or more of the fishermen made at least two deliveries, it is improbable that there was a significant number of completely unsuccessful fishermen. We have, then, the following rule: A fisherman is considered to have fished during a given week even though he made no deliveries, if he made one or more deliveries during the preceding or succeeding week, and at least 10 percent of the fishermen making deliveries during the given week made only one delivery.

This rule was adopted with the full realization that its use provides an approximate method only, and introduces some error. Nevertheless, the method should be sufficiently accurate where averages only are dealt with (as is the intention in the present analysis), even though in the cases of individual fishermen wrong decisions are occasionally made. Further, the method is certainly superior to completely disregarding zero catches, and appears to be about the best practicable procedure applicable to the available data.

When the actual calculations were being made it was seen that application of the rule to the data for the fall season would lead to highly erroneous results. The reason for this lies in the fact that near the end of the season fishermen are rapidly dropping out of the fishery. Examination of the data leads to the conclusion that in the fall the fishermen stop fishing for chinook salmon as soon as the catches begin to decrease markedly, so that there is little likelihood of any significant number of fishermen fishing as much as a week without making catches. In view of this finding it was decided not to attempt any estimation of zero fishing weeks during the fall season (weeks 20–22).

CALCULATION OF INDICES

Using the criterion of consistency and the method of estimating zero catches described in the preceding sections, it is possible to make a series of individual fisherman-week comparisons for each of the pairs of seasons used in the chain from 1935 to 1945. As an example, the tabulation for the 1935–36 spring run comparison is presented in table 3. The sum of the four totals for 1935 is 50,942 pounds and for 1936 it is 47,462. Dividing the latter sum by the former gives 0.9317 as the ratio of 1936 to 1935 catch-per-unit-of-effort. Calculations were similar for all other seasons, except that no estimate of zero catches was included for the fall season comparisons, as mentioned under Estimation of Zero Catches (p. 370). A summary of the resulting ratios is given in table 4.

In order to calculate from the above ratios a series of indices of catch-per-unit, the year 1940 was selected as a "base year." The actual catch-per-fisherman-week was calculated for each part of the season in this base year, and the corresponding parts of the other seasons were linked to 1940 by means of the ratios in table 4; the resulting index values are given in table 5, and are shown graphically in figure 4.

The catch-per-unit index, although not a direct measure of abundance as will be brought out below, is roughly indicative of broad changes. The

TABLE 3.—*Individual fisherman-week comparisons for the 1935–36 pair of adjacent spring-run seasons. Zeros indicate weeks in which fisherman was assumed to have fished even though he made no catches (as described in text under "Estimation of Zero Catches")*

[Catches in parentheses are deleted because there were no catches in the corresponding weeks of the adjacent seasons with which to compare them]

Fisherman No.	Catches in pounds during week							
	1 (May 1–7)		2 (May 8–14)		3 (May 15–21)		4 (May 22–28)	
	1935	1936	1935	1936	1935	1936	1935	1936
1	653	630	334	496	61	204	216	364
2	693	630	883	253	438	310	895	405
3	------	------	(0)	------	57	0	246	37
4	2,698	1,702	1,900	528	478	392	947	424
5	759	988	121	186	202	51	143	223
6	1,185	1,643	609	584	414	158	513	668
7	0	585	216	212	431	191	847	99
8	665	1,180	496	261	231	174	425	466
9	------	(0)	0	152	52	74	42	89
10	77	40	0	103	83	0	22	85
11	1,128	1,594	38	360	188	21	36	501
12	857	688	166	475	237	275	248	186
13	0	263	138	636	0	216	142	162
14	463	393	95	560	376	348	793	0
15	------	(211)	------	(295)	0	48	175	149
16	526	1,094	581	251	387	279	702	233
17	26	76	(0)	------	------	------	0	0
18	------	(28)	------	------	(0)	------	26	0
19	251	230	50	125	0	44	0	80
20	------	------	------	------	0	0	31	17
21	(154)	------	(0)	------	------	(0)	0	140
22	215	212	47	188	143	0	299	34
23	478	487	146	215	0	55	143	305
24	1,065	543	160	245	83	209	464	275
25	------	------	------	------	0	100	562	470
26	------	------	------	------	0	0	114	83
27	533	493	231	292	80	0	73	62
28	1,252	749	532	658	493	417	663	626
29	536	561	279	312	97	81	150	147
30	462	807	111	137	286	70	241	129
31	------	(0)	------	(396)	0	362	669	289
32	------	(68)	0	61	51	123	239	155
33	805	1,175	534	194	313	187	573	323
34	951	1,233	387	55	169	77	564	726
35	143	131	117	27	209	143	294	307
36	526	762	212	272	142	335	405	186
37	(149)	------	(0)	------	------	(0)	0	170
38	------	(0)	0	137	418	38	0	305
39	23	87	54	158	0	8	180	88
40	0	556	46	115	190	30	174	133
41	(73)	------	(23)	------	183	36	349	474
42	62	832	467	174	141	273	616	366
43	1,159	1,617	480	510	497	200	829	0
44	142	0	0	171	301	0	428	231
45	215	218	471	63	173	27	160	38
46	(362)	------	(79)	------	179	0	72	241
Total [1]	18,548	22,249	9,901	9,166	7,783	5,556	14,710	10,491

[1] Exclusive of strike-outs.

TABLE 4.—*Catch-per-unit of effort ratios between fishing seasons (season n/season n–1)*

Seasons compared	Spring, May 1–28	Summer, May 29–July 30	Fall, July 31–Oct. 1	Season,[1] May 1–Oct. 1
1936–35	0.9317	0.7424	0.5901	0.6943
1937–36	1.1878	.8714	1.3822	1.2029
1938–37	.7721	.7571	.7851	.7766
1939–38	.7943	1.2613	1.2169	1.1729
1940–39	.1905	.4498	1.0503	.8184
1941–40	3.2106	1.7588	2.0217	2.0088
1942–41	.7513	.9294	.9796	.9687
1943–42	2.2384	.8888	.4693	.5276
1944–43	.5311	1.0324	1.5408	1.4049
1945–44	2.1024	.3996	.9791	.9495

[1] Obtained by adding the linked catches for the entire season before dividing.

season curve in figure 4 does not indicate any marked trend upward or downward; although the trend for spring and summer is generally downward, the reverse is true for fall. Insofar as the spring runs are concerned this finding is in agreement with the statement of Rich (1942) that the spring runs have declined to a much greater extent than the fall runs. His analysis of total catches, however, indicated some decline in the fall also;

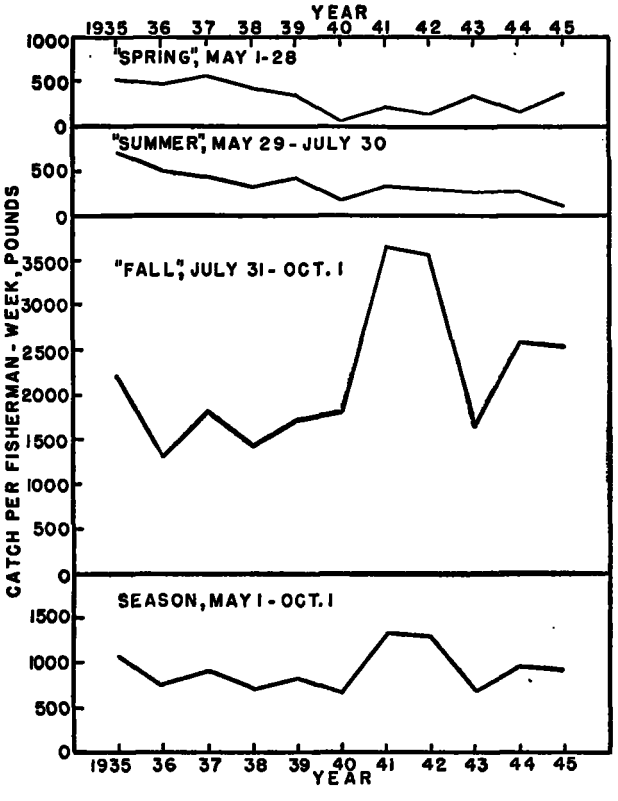

FIGURE 4.—Index of catch-per-unit-of-effort in zone 1 gill-net fishery for Columbia River chinook salmon.

the discrepancy may well be due to the difference in method of calculation.

FACTORS INFLUENCING ACCURACY OF INDEX

Changes in Efficiency of Gear

Although the chain-link method used in the above analysis eliminates the effect of variations in fishing efficiency among fishermen, it does not of course eliminate the effect of an increase in efficiency of an individual fisherman from one year to the next. Since most fisheries are undergoing some improvement in gear efficiency, the question of the magnitude of the effect of such improvement always arises in considering the accuracy of catch-per-unit indices like the present one.

TABLE 5.—*Values of catch per fisherman-week index, Columbia River chinook-salmon gill-net catches*

Year	Pounds per fisherman-week for—			
	Spring May 1–28	Summer May 29–July 30	Fall July 31–Oct. 1	Season May 1–Oct 1
1935	518	717	2,214	1,082
1936	483	532	1,307	751
1937	574	464	1,806	903
1938	443	351	1,418	701
1939	352	443	1,725	823
1940	67	199	1,812	673
1941	215	350	3,664	1,352
1942	162	326	3,589	1,310
1943	362	290	1,684	691
1944	192	299	2,595	971
1945	404	119	2,541	922

On this point, I think that the increase in efficiency of gill-net operations on the lower Columbia River from 1935 to 1945 was relatively slight. Although the selected fishermen did undoubtedly make minor improvements in their nets and boats, the only betterments of any significance were the increasing use of powerful, high-speed automotive-type boat engines in place of the old slow-speed low horsepower marine engines, and installation of power rollers on some of the 74 percent (Craig and Hacker 1940) of the boats which did not have them in 1935. To offset this, some of the 64 percent (*loc. cit.*) two-man boats undoubtedly changed to one-man operation (because it was more economical).

Because of the peculiar nature of the Columbia River gill-net fishery in zone 1, the extra speed gained by the installation of more powerful engines does not increase efficiency as much as it might in other fisheries. The many fish-receiving stations are so situated (fig. 1) that the fisherman

moors his boat and delivers his fish only a few miles from where he catches them, so that the time spent in straight (full speed) running or "driving" to and from the fishing spot is relatively small in relation to the length of the fishing night. The only other driving is done between sets of the net or drifts. On two separate fishing nights observed by me, only 21 percent of the total time of absence from port was spent in driving.

The effect of an increase in fishing intensity during the period covered by the study would be to make the catch-per-unit in the latter years higher than it should be relative to the early years. In view of the considerations mentioned above, however, I do not feel that the effect could have been large enough to seriously modify the results.

Ocean Troll Catch

The effect of the omission of high seas troll catches from the analysis has been mentioned in the introduction, and will be referred to again in Discussion and Conclusions. It is noted here only for emphasis.

Weighting of Data

Those statistically inclined will have noted that the method of calculating arithmetical averages used in obtaining the catch-per-unit index automatically weights the means according to the amount caught during each part of the season. On the whole this seems preferable to a system of equal weights, since in general the largest catches are made when the largest runs are passing through the fishery. In other words, it would not appear to be desirable to give the small summer run equal weight in determining the season's index to that accorded the heavy fall run. Any number of complicated systems for weighting data from different parts of the season in various ways could be devised, but in the absence of sufficient justification for using them they have not been tried.

Short Weeks

Weekly periods adjacent to closed seasons do not in all cases contain 7 days (for instance, period 17 actually contains only the 5 days August 21–25) and, therefore, do not always contain a Sunday. Thus every 6 years (not 7 because of leap years) there is one comparison for which week 17 of the first year will have 5 days and week 17 of the second year will have 4 days. However, also once every 6 years, there is a comparison in which the reverse is true; thus tending to compensate for the error introduced.

It should be noted in this connection that Rich (1942: 128) points out that the Sunday closed period is offset to a large extent by increased catches during the early days of the week.

Sources of Error

To recapitulate, changes in efficiency of gear, fluctuations in the ocean troll catch, weighting of data and unequal lengths of short weeks all have some influence on the accuracy of the catch-per-unit index. Of these, the troll fishery is the only one I feel to be important, as the others tend to be insignificant or compensatory in effect. Unfortunately, data are not now available by which the effect of the troll fishery on the index can be appraised. Even if it should prove to have an important effect, we still have a measure of catch-per-unit from the runs as they enter the river, and this is valuable in itself.

CALCULATION OF EFFORT EXPENDED

The application of modern methods of estimating abundance requires data on the amount of fishing effort expended each season. This can readily be calculated once an index of catch-per-unit-of-effort is available simply by dividing the total catch (table 6) by the catch-per-unit. The resulting statistics will be in terms of the unit used in the catch-per-unit calculation, or gill-net-fisherman-weeks of the 1940 season in the present study.

Since the catch-per-unit analysis was confined to waters inside the mouth of the Columbia, only the inside catches have been used in calculating effort expended. The total amount of effort so obtained actually includes that expended by traps, seines, set nets, and dip bag nets; it is nevertheless all expressed in gill-net units, just as the power of a gasoline engine may be expressed in units of horsepower.

In table 7 and figure 5 are given the calculated amounts of effort expended (in the above mentioned units) for each of the parts of the fishing season, and for the entire year. The graphs of figure 5 indicate that in general the trend of fish-

ing effort was downward during the period covered. This is contrary to the widespread impression that fishing effort has been steadily increasing. It is of course possible that increases in efficiency of gear might offset some of the apparent decline, but it hardly seems reasonable that they would be sufficient to nullify the 16 percent decrease from the average of the first 6 years to that of the last 5.

TABLE 6.—*Landings of chinook salmon inside the Columbia River*

[Thousands of pounds]

Year	Spring, May [1]	Summer, June–July [1]	Fall, August–September [1]	Entire year
1935	2,483	4,904	7,596	15,172
1936	2,093	3,661	9,815	15,998
1937	1,608	2,927	11,760	18,604
1938	1,708	2,222	8,315	12,598
1939	1,660	3,420	8,384	13,701
1940	657	1,998	10,721	13,770
1941	852	2,113	19,376	23,617
1942	951	1,496	15,954	19,061
1943	1,154	929	9,021	11,547
1944	647	1,254	11,749	14,308
1945	920	546	10,757	13,287

[1] Catch data were obtained from the fisheries departments of the States of Oregon and Washington, which sum them by calendar months. The months indicated vary only a few days from the actual periods used in the catch-per-unit analysis (table 5).

TABLE 7.—*Calculated amount of fishing effort expended toward the capture of chinook salmon inside the Columbia River, in units of 1940 gill-net fisherman-weeks*

[Thousands of pounds]

Year	Spring [1]	Summer [1]	Fall [1]	Entire year
1935	4,793	6,840	3,431	14,022
1936	4,333	6,882	7,510	21,302
1937	2,801	6,308	6,512	20,602
1938	3,856	6,330	5,864	17,971
1939	4,716	7,720	4,860	16,648
1940	9,806	10,040	5,917	20,461
1941	3,963	6,037	5,288	17,468
1942	5,870	4,589	4,445	14,550
1943	3,188	3,203	5,357	16,711
1944	3,370	4,194	4,528	14,735
1945	2,277	4,588	4,233	14,411

[1] See table 6 for explanation of these seasons.

The year 1940, particularly in the spring and summer seasons (table 7), is anomalous, and it was thought at first that this might be an artifact resulting from the method of estimating zero catches. In order to explore this possibility, the entire analysis for the spring and summer runs was recalculated, eliminating the estimation of zero catches. The recalculated data, however, still showed 1940 to represent as much of an anomaly as it did in the original figures, and it must be concluded that the unusually high amount of effort indicated for that year represented a real increase.

As mentioned previously, a May 20 through June 10 closed season was imposed beginning with the year 1943, in order to protect the spring run and summer run. It reduced the number of fishing days in spring by about 30 percent and in summer by about 20 percent. Actually there was a drop from 1942 to 1943 in fishing effort expended for both spring and summer (fig. 5). It is also evident from figure 5, however, that equally sharp drops had occurred previously, so that there is some question as to whether the reduction in effort was really accomplished by shortening the season. From the biological standpoint, of course, the closed season may well afford a measure of protection to the very meager runs of May 20–June 10, and if so is justifiable on this basis alone.

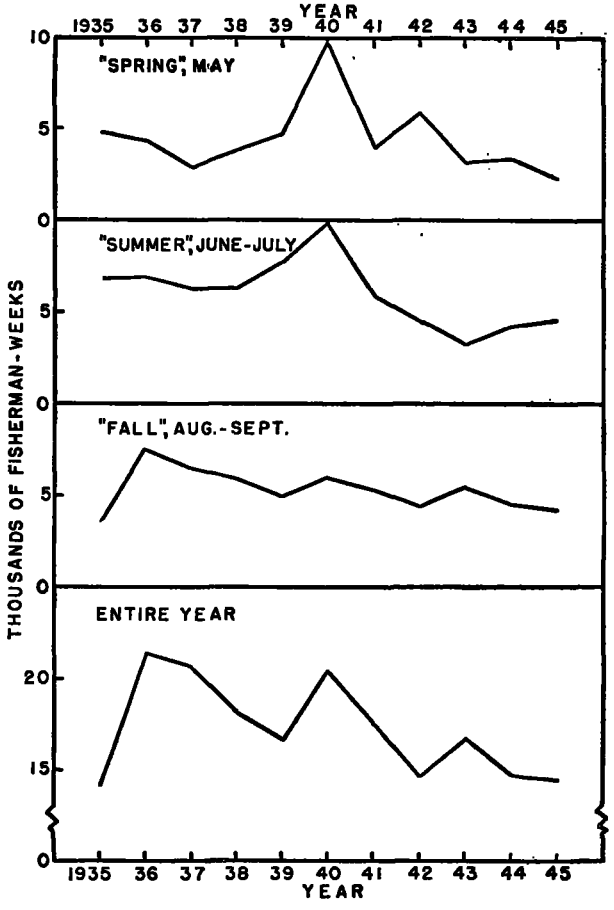

FIGURE 5.—Estimated fishing effort expended toward capture of Columbia River chinook salmon inside the river, in units of 1940 gill-net fishermen-weeks.

ESTIMATION OF TOTAL ABUNDANCE

Formulae and Assumptions

It has been very clearly demonstrated by various workers, particularly Ricker (1940, 1944), that a catch-per-unit-of-effort index is not ordinarily a direct measure of abundance of a fish population. In order to proceed from catch-per-unit to abundance it is necessary to make certain calculations, the type of calculation depending on the type of fishery. The type of fishery under consideration here is analogous to Ricker's (1944) type IA, in which there is assumed to be no significant natural mortality during the fishing season. In this type, providing absolute abundance is known for one of a pair of years, and total catch and total effort are known for both, it is possible to calculate the size of the stock for the second year by Ricker's (1940) formula (19):

$$\frac{f_2}{f_1} = \frac{\log\ (1-m_2)}{\log\ (1-m_1)}$$

where f= amount of effort expended and m= rate of exploitation or percentage of the stock taken by the fishery during the fishing season. In a later report (1944) Ricker shows this formula to be equivalent to an earlier one proposed by Baranov (1918).

$$\frac{f_2}{f_1} = \frac{p_2}{p_1}$$

where p is the instantaneous exploitation rate corresponding to the seasonal rate m.

Regarding the applicability of these formulae to anadromous fisheries, Ricker says in his 1940 paper:

> Such a fishery can be shown to conform to relationship (19) * * *, given the assumptions of (*a*) unchanging amount of fishing gear in use within each fishing season, and its uniform efficiency (or a reasonable approximation to these conditions); and (*b*) a uniform pattern of arrival and departure of the fish, between successive years * * *

As to (*a*), this can hardly be said to be true of the Columbia River fishery for chinook salmon. Data from table 6 show that the average numbers of fisherman-weeks expended during the 1935–45 period were 4,452 for spring, 6,066 for summer and 5,268 for fall. Since the respective average numbers of fishing weeks in these parts of the season were 3.7, 8.5, and 7.7 during 1935–45, the average numbers of units of gear (in terms of 1940 gill nets) in use for each were 1,203, 714, and 684, respectively. Whether or not these figures represent a reasonable approximation to uniformity is questionable, but it will be shown later that the calculation does yield more consistent results than the simple use of catch-per-unit. As far as assumption (*b*) is concerned, the data available (a series of detailed catches and counts at Bonneville Dam for the years 1938–43) indicate that, although there is some variation in migration pattern, it is relatively constant.

As stated above, we must have a measure of absolute abundance for at least 1 year in order to use the formula. Fortunately, it is not necessary to make a completely blind guess. In the year 1945 we have the Bonneville Dam (fig. 1) count and a reasonably accurate measure of the commercial river catch below Bonneville Dam (obtained by dividing the recorded catch in pounds by average weights based on samples taken throughout the season and in the various parts of the river, as see Silliman, Rich, and Bryant, 1948). It is only necessary to add to the sum of these an estimate of the number of fish spawning below Bonneville Dam, of which we have no count. Such an estimate has been made, based on actual stream observations of trained biologists and egg takes at hatcheries; a summary of the data is given in table 8. It would be preferable, in the abundance calculations, to deal entirely with numbers of fish, but this would preclude the extension of the series to years earlier than 1939, the earliest season for which adequate data on average weights (for converting catches from pounds to numbers) are available. The average weights of catches are therefore applied to escapements and counts, as set forth in table 8, thereby effecting a conversion of all data to pounds.

TABLE 8.—*Estimate of return of chinook salmon to the Columbia River in 1945*

Segment of return	Number of fish	Average weight of fish (pounds)	Pounds of fish
Catch below Bonneville Dam [1]	569,556	21.0	11,956,000
Estimated escapement below Bonneville Dam	70,000	[2] 21.0	1,470,000
Bonneville count	297,488	[3] 14.1	4,196,515
Total	937,044	18.8	17,622,515

[1] Exclusive of high seas troll catch.
[2] Assumed to be same as average weight of catch below Bonneville.
[3] Assumed to be same as average weight of catch above Bonneville.

The estimate of 1945 escapement below Bonneville Dam is admittedly subject to error, and this matter will be discussed further.

Calculations and Results

Although the data up to this point in the report have been dealt with by sections of the season corresponding to spring run, summer run, and fall run, the treatment hereafter will be confined to summaries for the entire year. It is felt that the determinations of abundance are not sufficiently precise to warrant their application to periods shorter than a full year.

The first step in the calculations is to obtain the seasonal rate of exploitation or fishing intensity, m, for 1945. Rounding the estimate from table 8, the total return is 17,600,000 pounds; the catch from table 6 is 13,287,000 pounds. Dividing catch by return gives 75.5 percent as the seasonal rate of exploitation. By means of tables such as those of Ricker (1944, table 1; 1948, appendix) such rates of exploitation can be converted to instantaneous mortality rates (this is done under the assumption that natural mortality is negligible during the salmon fishing season). The instantaneous mortality rate p corresponding to the seasonal rate of 75.5 percent is 1.41; it is used to facilitate the succeeding calculations. Such an instantaneous rate corresponds to n times the proportion of fish dying in one-nth of a season, when n is a very large number (actually p is the limit approached as n approaches infinity); in the present instance approximately 0.141 percent of the fish would die in 1/1000 of the season.

TABLE 9.—*Estimated seasonal rate of exploitation and return of Columbia River chinook salmon*

Year	Lower estimate		Median estimate		Upper estimate	
	Seasonal rate of exploitation, percentage	Return, 1,000 pounds	Seasonal rate of exploitation, percentage	Return, 1,000 pounds	Seasonal rate of exploitation, percentage	Return, 1,000 pounds
1935	81.6	18,600	74.6	20,300	68.6	22,100
1936	92.3	17,300	87.5	18,300	82.8	19,300
1937	91.7	20,300	86.6	21,500	81.7	22,800
1938	88.6	14,200	82.6	15,300	77.2	16,300
1939	86.6	15,800	80.2	17,100	74.6	18,400
1940	91.5	15,000	86.3	16,000	81.6	16,900
1941	87.9	26,900	81.7	28,900	76.3	31,000
1942	82.8	23,000	75.8	25,100	69.9	27,300
1943	86.7	13,300	80.4	14,400	74.8	15,400
1944	83.1	17,200	76.3	18,800	70.5	20,300
1945	82.5	16,100	75.5	17,600	69.6	19,100

By use of the formula $f_2/f_1=p_2/p_1$ given above, the value of p for 1944 can be calculated. Thus from table 7, the amounts of effort expended, 14,411 and 14,735 fisherman weeks for 1945 and 1944 respectively, give $f_2/f_1=1.0225$ (1944 is considered season number 2 in this calculation). Multiplying the 1945 value of p (1.41) by 1.0225 gives 1.78 as the 1944 value of p. By a series of similar calculations the series of p values is extended back to 1935. By the use of the aforementioned Ricker's tables these values of p are converted to values of m (percentage take of the fishery). Applying the values of m to the inside catches from table 6 gives a series of estimated poundage returns (median estimate) of chinook salmon to the Columbia River (table 9).

As noted previously, the estimate of 1945 escapement below Bonneville Dam is subject to error; we can, however, establish certain reasonable limits within which we can feel reasonably sure the true value lies. The lower limit is fixed, since the escapement cannot have been less than zero. There is, of course, no theoretical upper limit, but I feel that the accuracy of the estimated escapement is such that the actual escapement would not be greater than twice the estimated. The reasonable limits of error therefore can be established by using zero, or twice the estimate, for the escapement below Bonneville Dam. In the former instance we subtract the estimated below Bonneville escapement for 1945 (table 8) of 1,500,000 pounds from the estimated 17,600,000-pound total return to obtain a lower estimate of 16,100,000 pounds. In the latter instance the "below Bonneville" estimate is added instead of subtracted, giving a 19,100,000-pound upper estimate. The lower estimate and upper estimate were extended back to 1935 in the same manner as described above for the median estimate.

All three estimates are given in table 9 and figure 6. It is readily apparent from the figure that any one of the three estimates would lead to similar conclusions insofar as fluctuations in relative abundance are concerned, and it has been mentioned previously that relative abundance is the chief concern of this study. Because it uses the best available estimate of escapement below Bonneville, the median estimate series can be considered to contain the most probable estimates of return, and it will be used in the subsequent treatments of this report.

It was noted under Formulae and Assumptions that Ricker's (1940) postulate "(a)" of unchanging amount of gear during the season does not strictly hold for the Columbia River chinook fishery. This raises the question of the applicability of the formulae used in the calculations above. If the abundance estimate represents any improvement at all over the raw catch-per-unit index, then its use is justified. Such an improvement would be demonstrated if the abundance estimate were correlated more highly than the catch-per-unit index with a natural variable affecting the reproduction of salmon. A variable of this type, stream flow in the brood season, will be discussed below; it is pertinent to note here that the coefficient of its correlation with abundance estimate is 0.520, while with catch-per-unit index it is only 0.305. Thus, in addition to the logic of using the abundance estimate, there is the additional justification of improved correlation with a natural variable known to affect salmon spawning.

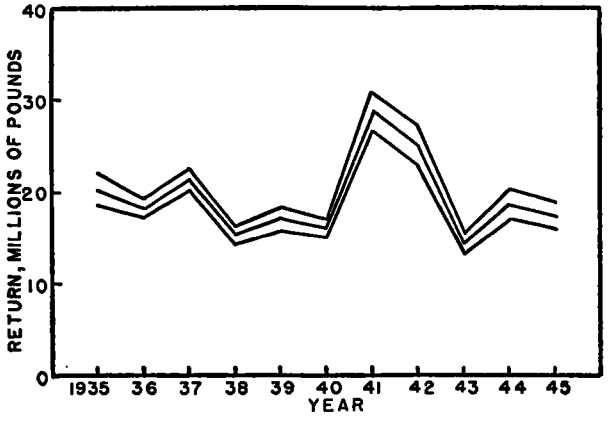

FIGURE 6.—Lower, median, and upper estimates of returns of chinook salmon to the Columbia River, derived as explained in the text.

FACTORS AFFECTING ABUNDANCE

Escapement and the Fishery

The escapement of mature salmon to the spawning beds is usually thought to be one of the major variables affecting the subsequent return; most salmon-fishery regulations are based on this idea. There have been few quantitative demonstrations of such a relationship, however, and beyond the recognized fact that there must be some seeding of the gravel beds to get any return, most of the remainder is conjecture. For the years of the present study an estimate of escapement is easily calculated by subtracting from the estimated returns in table 9 the inside catches in table 6; the resulting calculated escapements are given in table 10.

Since Columbia River chinook salmon are predominantly 4 years old when they return to the river, the return of any given year is linked to the escapement 4 years earlier. The data so linked are plotted as points on the scatter diagram of figure 7. Because of the 4-year lag in return, the 11 seasons of the analysis yield only 7 points. It is obvious from the figure that, within the range of escapements from 1935 to 1941, there was no close relationship between escapement and return. This does not, of course, mean that there is no relationship. We know, for instance, that at zero escapement there would be zero return, and that at some high escapement level the return must begin to decline. Apparently other factors affecting the return, and possible inaccuracies of measurement, obscure the true relation. The matter of the effect of other factors will be taken up again below under Stream Flow and Temperature.

TABLE 10.—*Estimated spawning escapement of chinook salmon in the Columbia River obtained by subtracting entire year catches in table 6 from median estimate of return in table 9*

Year	Escapement (thousands of pounds)	Year	Escapement (thousands of pounds)
1935	5,128	1941	5,283
1936	2,302	1942	6,039
1937	2,896	1943	2,853
1938	2,702	1944	4,492
1939	3,399	1945	4,313
1940	2,230		

It was shown in table 9 that the fishing intensities or rates of exploitation during 1935–45 were high, ranging from 75 to 88 percent, with a mean of 81 percent (median estimate), indicating a profound influence of the fishery on the escapement. Unfortunately, as shown above, the range of escapement covered in the present study is not great enough to indicate the relationship between escapement and return; therefore no relation (if such there be) between the fishery and return is demonstrable. It seems reasonably certain that if the calculations were carried backward to the earlier years of the fishery, such a relation could be shown to exist, because of the much wider range of fishing intensities that would be covered.

Since the escapement did not vary significantly during the period of study, as far as any demonstrable relation between escapement and return is concerned, the analyses below will be carried on as if the escapement were constant. This simplifies the calculations and permits the use of 11 instead of 7 pairs of observations in the correlations.

Stream Flow and Temperature

Stream flow is one of the natural variables known by direct observation to affect salmon reproduction. Its effect is felt in several ways.

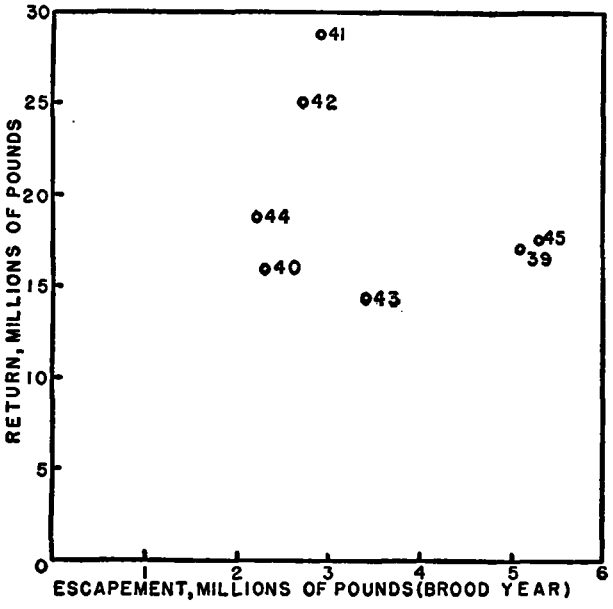

FIGURE 7.—Scatter diagram of estimated (median estimate) return against estimated escapement in the brood year (4 years before year of return). Numbers refer to year of return.

First, the upstream migrating salmon have much easier access to good gravel for spawning beds during years of high stream flow; many falls, and stretches of river affected by dams, are serious obstacles during low but not during high water. Second, high flows dilute polluted waters (such as those of the Willamette River near Portland) which during low water constitute barriers to both upstream and downstream migrants. Finally, high water during the hatching period is more favorable than low water to the escape of the fry from the gravel and their subsequent downstream migration.

In this study, therefore, we are not trying to determine whether or not there is any effect of stream flow. Salmon have actually been seen blocked during low-water periods. The purpose, then, is rather to attempt to assess the relative importance of this variable as compared with others known to affect salmon reproduction and survival.

TABLE 11.—*Stream-gaging stations whose records were used in calculating weighted mean run-off in the Columbia River chinook-salmon spawning areas*

Drainage	Estimated percentage of escapement [1]	Rivers	Gaging stations	
			Name	Number [2]
Grays River and Washington tributaries other than those listed below.	12	Cowlitz	Castle Rock, Wash.	1
Lewis and Kalama Rivers.	8	Lewis	Ariel, Wash.	2
Lower Oregon tributaries.	4	Sandy	Bull Run, Oregon (near).	3
Willamette River	10	Willamette	Salem, Oregon	4
Klickitat and Wind Rivers.	2	Klickitat	Pitt, Wash. (near).	5
Little and Big White Salmon Rivers.	6	White Salmon	Husum, Wash.	6
Deschutes and John Day Rivers and Upper Oregon tributaries.	2	Deschutes	Moody, Oreg.	7
Snake and Main Columbia Rivers.	51	Snake	Riparia and Clarkston, Wash. [3]	8, 9
Yakima River	2	Yakima	Cle Elum, Wash.	10
All tributaries above Rock Island Dam.	3	Wenatchee	Peshastin, Wash.	11

[1] Estimated on basis of stream surveys, counts at dams, and takes of eggs at hatcheries.
[2] Refers to map, fig. 8.
[3] Riparia to September 1935; Clarkston after September 1935.

A number of measures of stream flow are used, but the most convenient for the present study has been found to be the annual run-off in acre feet. This measure of total volume of flow is recorded by monthly units in the Surface Water Supply of the United States, papers of the United States Geological Survey. The data for the Columbia and its tributaries are contained in part 12, Pacific Slope Basins in Washington and Upper Columbia River Basin, and part 14, Pacific Slope Basins in Oregon and Lower Columbia River Basin. The records are available for a great number of stream-gaging stations, and some selection is necessary.

Gaging station records for this study were selected on the basis of continuity of record over the required period, and on adequate representation of the important salmon-spawning drainages. A total of 10 such stations was selected: Their location in relation to the estimated distribution of the chinook salmon escapement is indicated in table 11 and figure 8.

The selection of the "flow season" used was based on the facts of chinook-salmon life history. Mature adults of this species begin to enter the Columbia River tributaries around May 1, spawning takes place in the summer and fall, incubation in the fall and winter, and most of the down-stream migration into the main river is complete by April 30. Thus the flow season, May 1 through April 30, has been chosen for the calculation of seasonal run-off. The annual May–April run-off was determined for each of the stations in table 11, the sums weighted by the estimated percentage escapements also given in table 11, and the weighted mean calculated; results are given in table 12.

TABLE 12.—*Weighted mean run-off, season May 1–Apr. 30, Columbia River chinook-salmon spawning streams*

Season	Run-off (thousand of acre-feet)	Season	Run-off (thousand of acre-feet)
1931–32	14,890	1937–38	18,678
1932–33	19,946	1938–39	20,956
1933–34	24,692	1939–40	16,861
1934–35	13,219	1940–41	14,785
1935–36	17,002	1941–42	18,483
1936–37	15,860		

The weighted seasonal run-offs were paired with the estimated returns from table 9, 4 years later, that is, the 1931–32 run-off season was paired with the 1935 return; this was because, as mentioned above, chinook salmon are predominantly 4 years

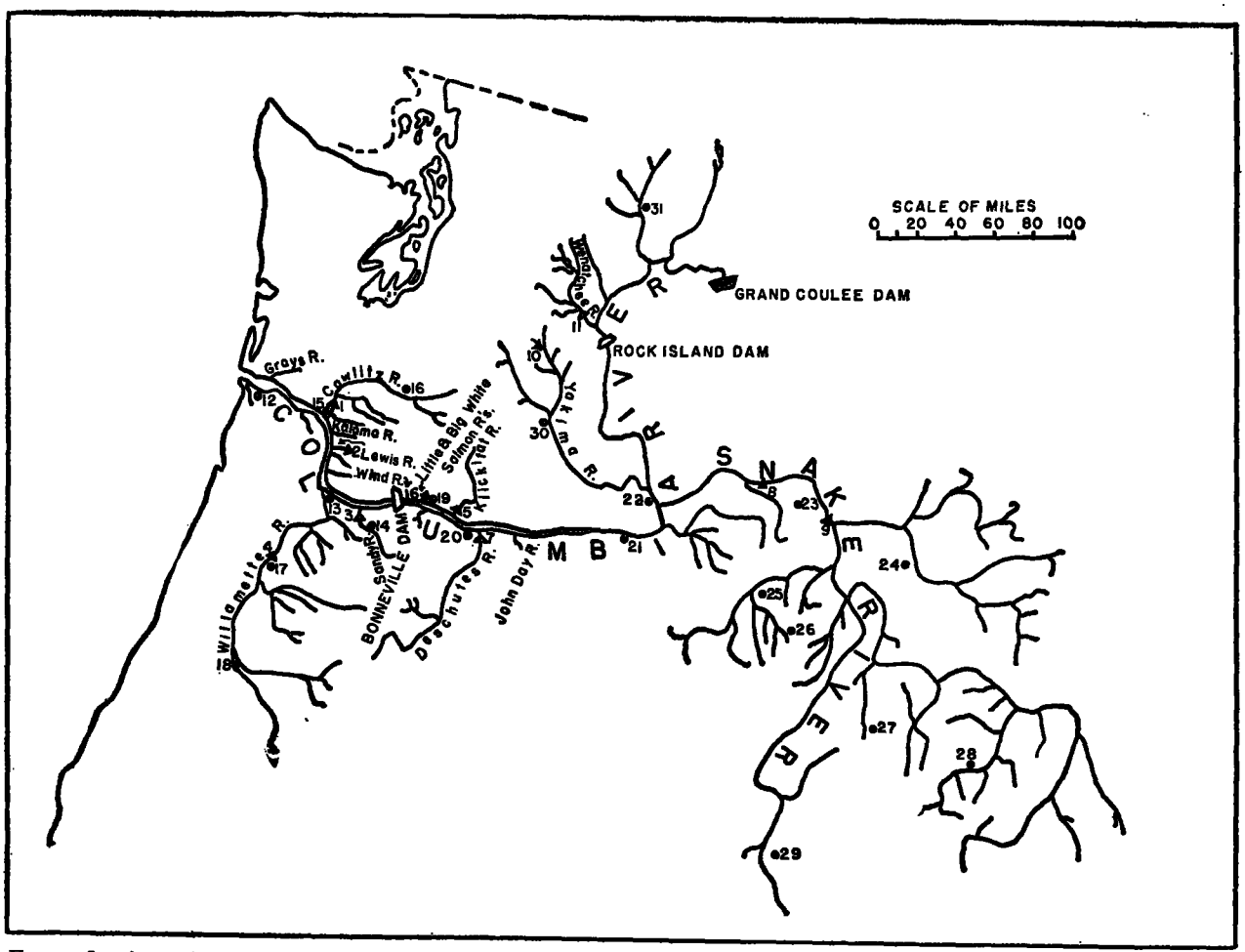

FIGURE 8.—Available (1944) salmon-spawning streams of the Columbia River showing location of stream-gaging (triangles) and temperature-observation (round dots) stations from which records were used in calculating weighted mean run-off and winter temperature. Numbers 1–11 refer to table 11, and 12–31 to table 13. Shows only parts of streams actually available for spawning.

of age (starting from egg deposition) when they return to the river. In figure 9 return is plotted against run-off, and the line of least-squares fit is shown. The coefficient of correlation is 0.520, and with 9 degrees of freedom the value of P is 0.1.

The above value of P would not ordinarily be considered to indicate a significant correlation. However, as stated, the purpose of the regression is to indicate relative rather than absolute effect. Statisticians consider that in a correlation the square of the coefficient indicates the proportion of fluctuations in the dependent variable associated with those in the independent variable; on this basis 27 percent of the fluctuations in return are associated with those in stream flow. The actual effect of flow on return is probably much greater than this, however, since the true relationship is obscured by such disturbing elements as variation in time and place of spawning, inaccuracies introduced by variable marine survival, and deviation from the 4-year spawning cycle. In regard to the last item, an analysis of the 2,677 returns from a marking experiment of Harlan B. Holmes showed that only about two-thirds of the returning fish were 4-year olds; the remaining one-third consisting of two-, three-, five-, and six-year olds.

Although winter temperatures are known to affect survival of salmon eggs (the possibility of

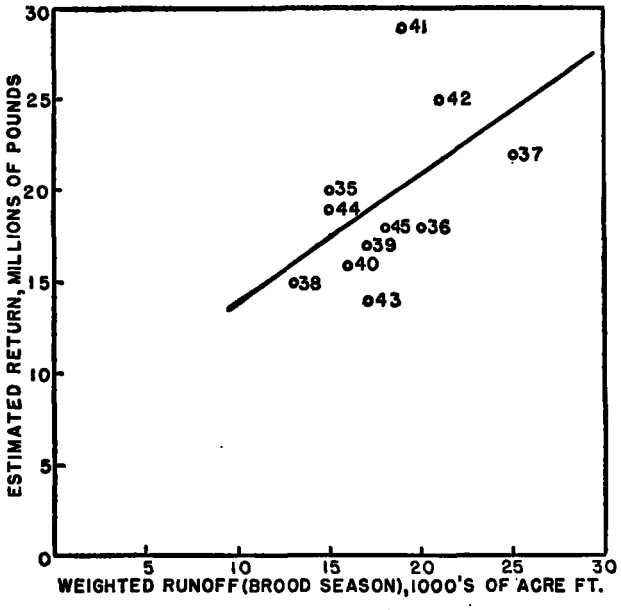

FIGURE 9.—Regression of estimated (median estimate) return on weighted May–April run-off in the brood season (4 years before year of return). Line shown is least-squares fit. Numbers refer to year of return.

such an effect on sockeye-salmon eggs in the Fraser River is pointed out by Rounsefell and Kelez 1938: 778), the relation is even more complicated than is the case with regard to stream flow. In general, severe winters result in some freezing of eggs. This effect is dependent to some extent, however, on the amount of protection afforded the spawning-nests or redds by snow cover. Also, in winters of alternate severe freezes and rapid thaws, there is damage to the redds through the scouring effect of the large ice cakes as they pass downstream. The net result of such effects is to obscure to a considerable extent any relation between winter temperatures in the brood season and the return 4 years later.

TABLE 13.—*Stations whose temperature records were used in calculating weighted mean winter temperature for Columbia River chinook salmon spawning areas*

Drainage	Estimated percentage of escapement [1]	Station	
		Name	No. [2]
Columbia River below Bonneville Dam, other than Willamette and Cowlitz Rivers.	14	Astoria, Oreg.	12
		Portland, Oreg.	13
		Headworks, Oreg.	14
Cowlitz River	10	Longview, Wash.	15
		Kosmos, Wash.	16
Willamette River	10	Salem, Oreg.	17
		Eugene, Oreg.	18
Little, Big White Salmon, and Snake Rivers, and the main Columbia River between Bonneville Dam and Rock Island Dam.	57	White Salmon, Wash.	19
		The Dalles, Oreg.	20
		Umatilla, Oreg.	21
		Kennewick, Wash.	22
		Pomeroy, Wash.	23
		Nezperce, Idaho	24
		Cove, Idaho	25
		Joseph, Oreg.	26
		New Meadows, Idaho	27
		Challis, Idaho	28
		Parma, Idaho	29
Tributaries between Bonneville and Rock Island other than Snake, Little, and Big White Salmon Rivers.	6	Yakima, Wash.	30
Main Columbia River and tributaries above Rock Island Dam.	3	Winthrop, Wash.	31

[1] Estimated on basis of stream surveys, counts at dams, and quantities of eggs taken at hatcheries.
[2] Refers to map, fig. 8.

Nevertheless, such a relation is of interest, and the appropriate data have been analyzed. Monthly average temperatures are given in the annual summaries of the series Climatological Data issued by the United States Weather Bureau. A total of 20 representative stations listed in the Oregon, Washington, and Idaho sections of the summaries was selected; criteria of selection were the same as mentioned for stream-gaging stations. A list of the stations is given in table 13, and their location is shown in figure 8. Simple averages of the December through February means were calculated

(table 14); weighting in accordance with estimated percentage distribution of chinook salmon escapement was achieved by making the numbers of stations in each drainage proportional to such percentage.

TABLE 14.—*Weighted average winter (December through February) temperatures for Columbia River chinook salmon spawning areas*

Winter	Temperature (° F.)	Winter	Temperature (° F.)
1931–32	31.1	1937–38	37.3
1932–33	30.3	1938–39	34.9
1933–34	40.8	1939–40	37.4
1934–35	36.4	1940–41	37.0
1935–36	30.9	1941–42	32.7
1936–37	28.4		

Pairing of winter temperature seasons with return years was done in the same manner as with stream flows (described above) and a regression of return on temperature was made (fig. 10). The coefficient of correlation (0.337) for the least-squares line shown does not indicate significance in the statistical sense. Here again, however, the true nature of the relation has been obscured by other variables. In addition to those mentioned in connection with stream flows, and in the paragraph before the preceding one, there are many other minutiae of the relationship which cannot be recognized in a general, over-all treatment like the present.

Obviously, more detailed study of the effects of both stream flow and temperature would be necessary for an accurate appraisal. About all the studies presented herein accomplish is to indicate the relative importance of the two variables. Taking the squares of the correlation coefficients (0.270 for stream flow and 0.114 for temperature), it would appear that stream flow is about twice as important as temperature in affecting fluctuations in return, within the range of flows and temperatures experienced during the period of the analysis. Because of the rough nature of the relationships found, they were not combined into a multiple regression for the purpose of more precisely determining relative effect of the two independent variables.

If the relations of return with stream flow and temperature could be more exactly defined, it would probably be found that they were curvilinear rather than rectilinear, and that a leveling off occurred at both high waters and high winter temperatures. The reason for expecting this lies in the fact that once streams are high enough to prevent blockage of fish, and once winters are warm enough to avoid freezing of eggs, there is little or no improvement from further increases. It is entirely possible, in fact, that at high enough temperatures and flows reproduction of the salmon would actually be impaired, so that the curves would have a descending as well as an ascending limb.

It was mentioned above under Escapement and the Fishery that such variables as flow and temperature might obscure the relation between escapement and return. By use of the regression lines of figures 9 and 10, it is possible to make an adjustment of the return data which will partially eliminate the effect of variations in stream flow and temperature. This is done by computing the deviation from mean return of the points on each of the regression lines corresponding to each yearly flow and temperature, and subtracting these deviations from the original "raw" returns.

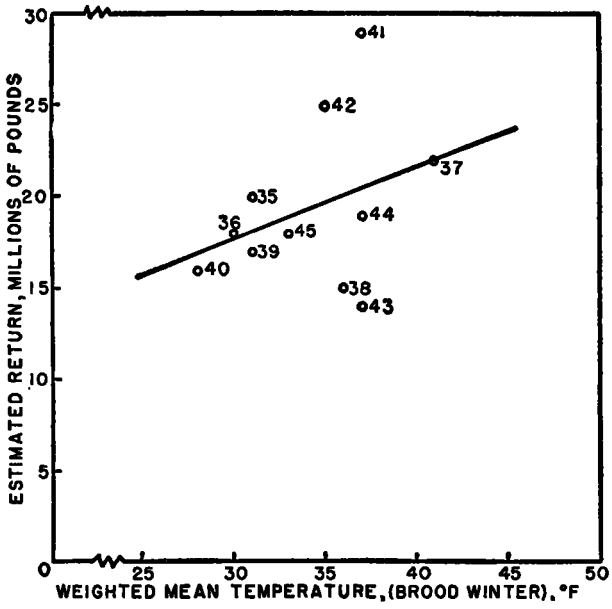

FIGURE 10.—Regression of estimated (median estimate) return on weighted winter temperature in the brood winter (4 years before year of return). Line shown is least-squares fit. Numbers refer to year of return.

The calculated weather adjustments, along with the unadjusted and adjusted returns, are given in table 15, covering the return years of the scatter

diagram of figure 7. A new diagram of escapement-return relation, using the adjusted returns, is shown in figure 11. Obviously an insufficient proportion of the disturbance of extraneous variables has been removed to bring out the real nature of the relationship; a significant escapement-return relation has still not been demonstrated.

Dams

As a result of the completion in recent years of such huge structures as Bonneville Dam and Grand Coulee Dam, and the imminent construction of several others of similar proportions, much controversy has arisen as to the effect of such projects on the runs of salmon. Although the loss of spawning ground above Grand Coulee Dam has been compensated for by transference of runs to other streams (Fish and Hanavan 1948), there have been claims that Bonneville Dam, despite the fishways in operation there, has caused a decline in the runs. Indeed, Harlan B. Holmes has reported some loss of juvenile salmon as they pass downstream over the dam and through the turbines, but the ultimate effect of this on the returns is not yet clearly understood.

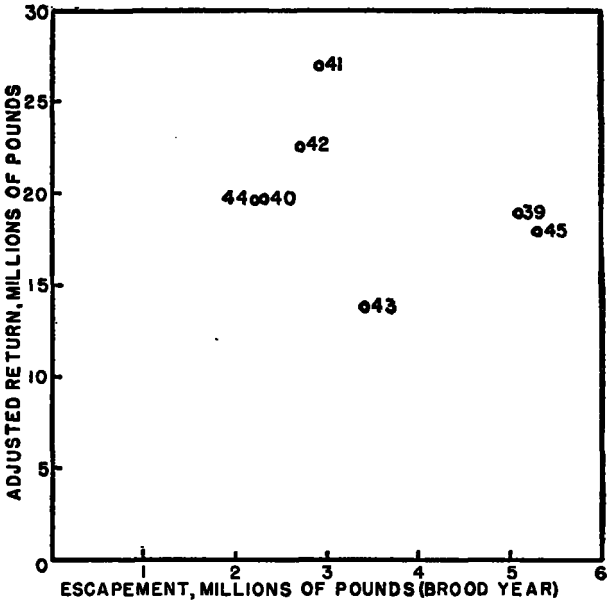

FIGURE 11.—Scatter diagram of estimated (median estimate) return, adjusted for effect of stream flow and temperature, against estimated escapement in the brood year (4 years before year of return). Numbers refer to year of return.

TABLE 15.—*Adjustment of median estimate returns for effect of stream flow and temperature*

[All data are in millions of pounds]

Year of return	Unadjusted returns	Adjustment for stream flow	Adjustment for temperature	Adjusted returns
1939	17.1	+0.6	+1.3	19.0
1940	16.0	+1.3	+2.4	19.7
1941	28.9	−.8	−1.1	27.0
1942	25.1	−2.2	−.3	22.6
1943	14.4	+.6	−1.1	13.9
1944	18.8	+2.0	−1.1	19.7
1945	17.6	−.1	+.5	18.0

Some light might be thrown on the question by comparing the returns of chinook salmon to the Columbia River before and after 1942 (Bonneville Dam was completed in 1938, and the chinook salmon return predominantly as 4-year fish). From table 9 the average median estimate return for the years 1935–41 is 19,600,000 pounds, while for 1942–45 it is 19,000,000 pounds. This slight decrease is shown by Student's (Fisher 1941) t test not to be significant ($P=0.8$).

Perhaps a better way to appraise the effect of Bonneville Dam, although it is sacrificial of data, is to analyze the ratios of returns from escapements before and after completion of the structure. The comparable returns and escapements, and the ratios between them, are given in table 16. The mean ratio of return for 1935–37 escapements is 6.75, and for 1938–41 it is 6.32. Here again Student's t test shows the small difference not to be significant ($P=0.8$).

Thus, as far as the present study is concerned, no significant effect of Bonneville Dam can be demonstrated. The loss of downstream migrants alluded to above, however, indicates that there must have been some effect; it is no doubt obscured in the data of this report by the effects of other variables.

TABLE 16.—*Estimated escapements and returns, for corresponding years, of Columbia River chinook salmon, and ratios of return to escapement*

[All data are in millions of pounds]

Year of escapement	Escapement	Year of return	Return	Ratio, return escapement
1935	5.13	1939	17.1	3.33
1936	2.30	1940	16.0	6.96
1937	2.90	1941	28.9	9.97
1938	2.70	1942	25.1	9.30
1939	3.40	1943	14.4	4.24
1940	2.23	1944	18.8	8.43
1941	5.28	1945	17.6	3.33

Anomalous Seasons

Throughout the various regressions studied above, two fishing seasons more than any others have failed to conform to the indicated relationships; 1941 has been invariably "high" and 1943 invariably "low" (figs. 9 and 10). If these seasons were eliminated from the regressions the correlations would be greatly improved. Such elision, however, is not justifiable unless it can be supported on valid *a priori grounds*. In the present instance no such grounds could be found, and the anomalous years were of necessity included with the rest of the seasons in the regressions. Further detailed study of the survival conditions in the corresponding brood seasons (1937–38 and 1939–40) should be made in order to determine the reasons for the anomalously high and low returns.

A suggestion as to the direction which such a study might follow has been made by Dr. L. A. Walford. He has pointed out to me that there is a general correspondence between salinities off California, as reported in his study of the relation between salinity and year-class strength in the sardine (Walford 1946), and the returns of salmon two years later. It is particularly noteworthy in connection with the anomalies mentioned above that the highest and lowest salinities reported in Walford's paper occur in 1939 and 1941, respectively. If the condition reflected in these salinities is coastwide, and if this condition encourages the growth of organisms on which salmon feed, a valid relationship may readily be postulated. With the present data it is not possible to obtain a significant correlation, but further study of the relationship should be made.

DISCUSSION AND CONCLUSIONS

One of the objectives mentioned in the introduction was to set forth in detail methods of calculating catch-per-unit-of-effort and of estimating abundance. It is believed that the second, third, and fourth major sections of this report present a sufficiently detailed explanation that anyone studying them can reproduce the calculations. Further, it is felt that the methods used are flexible enough so that they may be applied in other seasons and to other species of salmon.

The abundance index for chinook salmon should be extended back to the beginning of the available record at the earliest practicable moment (the writer was prevented from doing so by extraneous circumstances). When this has been done it will be possible to study the effect of changes in fishing intensity and other variables much greater than any that occurred during the 1935–45 period of the present report. Years subsequent to 1945 should also be added as soon as the data become available, in order to provide a continuing measure of abundance for current information.

The second major objective was to make a preliminary appraisal of factors influencing fluctuations in abundance. Four such variables have been considered: (1) The fishery through its effect on escapement, (2) stream flow through its effect on upstream and downstream migration, (3) winter temperature through its effect on survival of the incubating eggs, and (4) dams through their effect on upstream and downstream migration. It has been shown that the data of this study do not indicate any effect of (1) and (4) during the period covered, although there are undoubtedly effects which are obscured in the data by other variables.

Stream flow and temperature may be positively associated, but data were insufficient to establish a statistical significance. As both variables are known by direct observation to affect salmon reproduction, the correlations may be used as rough relative measures of the respective effects on fluctuations in return of adult salmon. Stream flow appeared to be about twice as important as temperature.

Regarding the course of abundance levels in general, the curves of figure 6 certainly do not indicate any well-marked trend, either upward or downward. Values of the catch-per-unit index (fig. 4) for the various parts of the fishing season (roughly indicative of broad changes in abundance level) show a decline for the spring and summer runs offset by an increase for the fall run. This finding is in keeping with current theories of fishery biologists studying the Columbia River salmon runs.

It is well in conclusion to reiterate once more the fact that this study has applied only to the chinook-salmon runs as they enter the river. The large ocean-troll-fishery takes its toll of the fish before they arrive at the locale of the analysis, and this toll may well have a considerable effect on abundance. Unfortunately, data susceptible of an abundance analysis are not available for the troll fishery for the period of this study.

SUMMARY

1. The source material of this study consists of cannery-ledger entries indicating the daily deliveries by certain selected gill-net fishermen, in pounds of chinook salmon, to receiving stations in the lower part of the Columbia River.

2. "Zero catches" were estimated on the basis that a fisherman would be considered fishing during a given week even though he made no catch, providing he made deliveries in either the preceding or the succeeding week, and providing that at least 10 percent of the other fishermen made only one catch.

3. Deliveries were summed in weekly units and compared with those of adjacent seasons, week by week and fisherman by fisherman.

4. Catch-per-fisherman-week data were linked into a series covering the 11 seasons 1935–45, using the "chain-link" method.

5. Total fishing effort expended in the Columbia River, in terms of 1940 gill-net fisherman-weeks, was computed by dividing the "inside" river catch by the catch-per-fisherman-week, for each year. In general the expenditure of effort was declining during the period of the study.

6. Catch-per-unit-of- effort index was converted to estimated size of return by use of the formula $p_2/p_1=f_2/f_1$, where f is fishing effort and p is "instantaneous rate of fishing mortality."

7. Estimated returns varied from 14.4 to 28.9 millions of pounds, with a mean of 19.4.

8. Estimated fishing intensity varied from 75 to 88 percent, with a mean of 81 percent.

9. Calculated escapements ranged for 2.23 to 6.04 millions of pounds. This range was not sufficiently great to permit the demonstration of a relationship between escapement and return.

10. Positive correlations (not statistically significant) suggested that stream flow is about twice as important as winter temperature in affecting fluctuations in return.

11. Ratio of return to escapement varied from 3.33 to 9.97, with a mean of 6.51.

12. No significant effect of Bonneville Dam could be demonstrated, either by comparing returns or by comparing ratios of return to escapement.

13. The season of 1941 was invariably high and 1943 invariably low in all regression treatments. A possible relation of these anomalies with ocean salinities is suggested.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

APPARENT ABUNDANCE OF THE PILCHARD (*SARDINOPS CAERULEA*) OFF OREGON AND WASHINGTON, 1935–43, AS MEASURED BY THE CATCH PER BOAT

BY JOHN C. MARR

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APPARENT ABUNDANCE OF THE PILCHARD (*SARDINOPS CAERULEA*) OFF OREGON AND WASHINGTON, 1935-43, AS MEASURED BY CATCH PER BOAT

By JOHN C. MARR, Aquatic Biologist

One of the basic problems in fishery biology is the formulation of estimates of abundance. Boat-catch data constitute a source upon which such estimates are based. In general, it may be stated that the amount of fish taken by a fishery depends on the quantity of fish in the sea (abundance), the accessibility of the fish to the fishermen (availability) and the amount of effort (boat-weeks or similar units) expended in the fishery. Abundance is determined by the amount of successful reproduction (which may, and often does, take place at a considerable distance in space and time from the fishing grounds) as subsequently influenced by natural and fishing mortality. Availability is probably determined by conditions on the fishing grounds at the time the fishery is being prosecuted. It includes the possibility of migration of the fish to or from the fishing grounds. The quantities of fish which may be caught per unit-of-effort by the fishermen are thus determined by the combined effect of varying availability and fluctuations in abundance. The term "apparent abundance" is introduced to represent this combined effect.

Since the start of a fishery for the pilchard or sardine, *Sardinops caerulea* (Girard) 1854, in Oregon and Washington, boat-catch data (date, location, and amount of catch, name of boat, and other information not used here) have been collected by the fishery agencies of these States. If these catch data are converted to catch per unit-of-effort, the relative changes from season to season will be a measure of the changes in the level of apparent abundance or, possibly, changes in the amount of effort expended.

The first pilchard cannery in California was in operation before 1900 and large scale commercial operations started in 1916. The industry in British Columbia also is comparatively old; the first pilchard cannery there was in operation in 1917. In contrast, the Oregon pilchard fishery began only in 1935. This fishery started as a result of modification of laws concerned with the use of food fishes for reduction purposes (Hoy 1938: 5), rather than a sudden change in the habits or distribution of the pilchard. Similarly, the pilchard fishery in Washington began in 1936 as a result of special legislation (Chapman 1936: 1). In the beginning, landings were made at Coos Bay, Astoria, and Grays Harbor; however, at Coos Bay they were discontinued after 1938.[1] The original boat-catch data for the years involved are not given because of space limitations. Data on the tons landed in each season are shown in table 1 and in figure 2.

There are marked differences among the methods of purse seining for pilchard in the several fishing areas along the Pacific Coast of North America. Catches in British Columbia are usually made during the day, "with the best results usually obtained at daybreak and dusk" (Hart 1933: 13). (This refers to catches made off the Canadian coast; in some later years the Canadian fleet has often fished off the United States coast.) The Canadian boats fish in pairs (one seine boat and one tender) whereas in all other regions the boats operate singly. Catches landed at Grays Harbor and Astoria are made during daylight hours. Catches landed at Coos Bay were made both day and night. Pilchard landed at California ports are almost always caught at night and mostly in the dark of the moon. Hart (1933: 13), with reference to the Canadian fishery, states that "Night fishing is precluded by the damage which is done to the nets after dark by the dogfish." Chapman (1936: 5), speaking of the 1936 season in Washington, states that "the fishermen say that the fish split up into small schools of 5 and 10 tons at night, for which it is not practical to set. In addition,

[1] "Since writing the above, I have been informed by D. L. McKernan of the Oregon Fish Commission that some landings were also made at Coos Bay in 1939. Actually, 6 boats made 17 landings, or about 3 percent of the Oregon landings and 1.7 percent of the Oregon-Washington landings for that year. Under the methods of season and fleet definition used, these would be reduced to 1.4 percent and 0.8 percent, respectively."

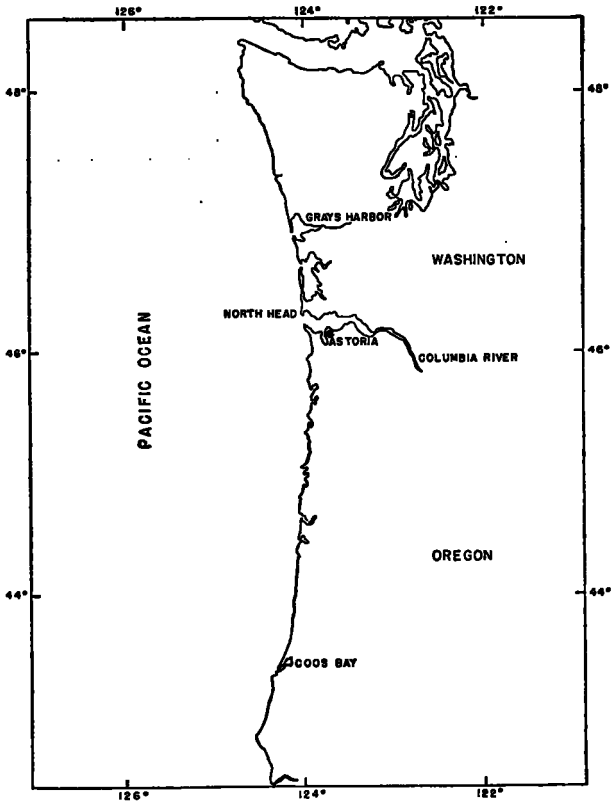

FIGURE 1.—Chart of locations mentioned in the text.

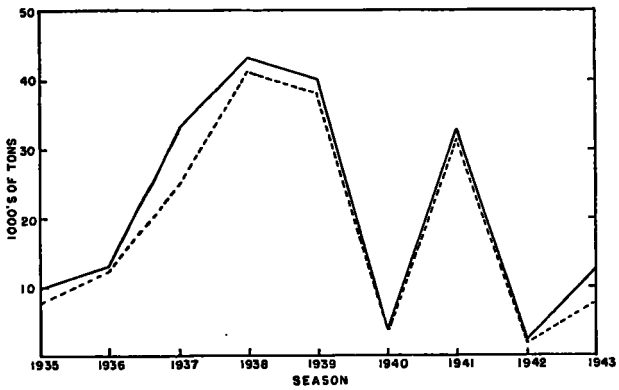

FIGURE 2.—The solid line indicates the total number of tons of pilchard landed at Astoria and Grays Harbor from 1935 through 1943; the dashed line indicates the number of tons landed by the selected fleet during the seasons as defined in the text.

in the northern area near Swiftsure Bank, the dogfish are so thick after dark that they greatly hinder fishing." California fishermen are not troubled by this shark.

The California fishery operates at night, apparently because of the presence in the water of large numbers of luminescent planktonic organisms. The mechanical stimulation of these organisms by the pilchard results in a milky glow which makes the schools easier to locate by night than by day (N. B. Scofield 1928: 250; W. L. Scofield 1926: 16) and also probably renders the gear more effective. Luminescent organisms are also present in the more northerly waters, although possibly not in such vast numbers (Sverdrup, Johnson, and Fleming 1942: 833). The presence or absence of large numbers of dogfish may determine whether pilchard are fished for in the day time or at night. However, it seems probable that there is a fundamental difference in the behavior of the pilchard on the different fishing grounds. In the south there may be a tendency for the fish to concentrate in schools at or near the surface, at night and to disperse horizontally or vertically during the daytime, or to descend without dispersing during the daytime. The reverse may occur in the more northern waters. If this situation actually obtains, Coos Bay may lie in a transition area. Observations in the several regions would be of great value and comparative studies of the northern and southern regions might well be a profitable method of obtaining information as to some of the factors that control the availability of the fish to the fishermen.

The data in this study have been made available through the courtesy of the Oregon Fish Commission and the Washington Department of Fisheries. V. E. Brock has completed a study of the first 4 years of this fishery and, although this analysis takes a different form than his, he generously made his work available. M. B. Schaefer, O. E. Sette, R. P. Silliman, and L. A. Walford have given freely of their time and advice.

CATCH PER STANDARD BOAT-WEEK

Catch per unit-of-effort might be most simply measured by the average number of tons of fish caught per boat per week. The use of such a measure would assume that the amount of effort expended per week were the same for all boats and for every year. This assumption is not valid, due to changes in sizes of boats in the fleet and related changes in nets that occur over a period of years. Further complications arise in the systematic treatment of the present data as a result of the irregular nature of the seasons each year. These are not fixed by law but are determined by the movements of the fish, by the weather, by the

success of the California fishery, and probably other factors such as the economic problems resulting from processing pilchard early in the summer when the fat content usually is low.

In order to facilitate the treatment of the data certain rules had to be made. These are as follows:

1. Data for Coos Bay are omitted from this study, since no landings were made there after 1939 [2] and because catches landed there were made both day and night. A single landing during a season at Coos Bay by a boat making all of its other landings at Grays Harbor or Astoria was treated as though it had been made at the customary port. However, boats making two or more landings at Coos Bay during a season were eliminated.

2. Boats fishing out of Grays Harbor and Astoria fished in essentially the same areas and, in fact, often made landings at both ports. The percentage of boats making landings at both ports during a season ranged from 11 to 90 percent over the nine seasons covered. Therefore, in treating the data, boats from the two ports were considered to belong to one fleet.

[2] See footnote 1, p. 385.

3. In order to minimize error or possible bias due to the catches of boats which were in the fishery for a short period not necessarily representative of the season as a whole, all boats which landed fish in less than one-half the number of weeks in a season were omitted.

4. Scattered landings, which characteristically preceded and followed the period of a few weeks when the bulk of the catch was made each year, were discarded. This had the effect of keeping in the data many boats that would have been discarded under rule 3. To eliminate these scattered landings required a certain amount of arbitrary judgment, but it was done in a manner aimed at maximizing both length of season and number of boats. In no year did the landings preceding or following the season thus defined, as the period containing the bulk of the landings, amount to more than 8.1 percent of the total landings.

5. Within the limits of these seasons there is no way of telling whether or not a boat was fishing during periods in which it made no landings. Therefore, if a boat made no landings during a particular week, it was assumed to be fishing provided that (*a*) it made landings in the weeks immediately preceding and following that week, and

TABLE 1.—*Information on the Oregon-Washington pilchard fishery, 1935 through 1943*

Season	Dates of first and last landings	Dates of season	Number of weeks in season	Total number of landings	Landings omitted						
					Number outside of season [1]	Percentage outside of season	Number at Coos Bay [2]	Number less than one-half season [3]	Number with no length data [4]	Total number	Total percent
1935	June 23 to Nov. 30	July 7 to Sept. 14	10	139	9	6.5	6	23	0	38	27.3
1936	July 15 to Sept. 30	July 19 to Aug. 29	6	247	17	6.9	2	16	4	39	15.8
1937	July 9 to Oct. 13	July 18 to Sept. 25	10	455	37	8.1	0	55	0	92	20.2
1938	July 29 to Sept. 19	July 31 to Sept. 10	6	607	14	2.3	16	11	0	41	6.8
1939	July 7 to Aug. 17	July 9 to Aug. 19	6	626	6	1.0	0	18	18	42	6.7
1940	Aug. 5 to Sept. 21	Aug. 4 to Aug. 17	2	63	3	4.8	0	0	4	7	11.1
1941	June 21 to Sept. 3	July 6 to Aug. 30	8	610	32	5.2	0	18	0	50	8.2
1942	June 30 to Aug. 7	June 28 to Aug. 8	6	57	0	----------	0	13	0	13	22.8
1943	July 8 to Aug. 16	July 11 to Aug. 21	6	170	2	1.2	0	23	41	66	38.8

Season	Total tons landed at Astoria and Grays Harbor	Total tons landed at Coos Bay [5]	Percentage of Astoria and Grays Harbor landings omitted	Number of boats in fishery	Number of boats in selected fleet	Average length selected fleet	Number of boat weeks
1935	9,915	15,988	20.7	11	6	70	43
1936	13,019	7,663	13.5	33	26	69	113
1937	33,106	759	25.7	29	16	72	135
1938	43,155	554	4.4	62	57	73	288
1939	40,109	----------	5.0	64	55	73	278
1940	3,890	----------	11.9	36	33	73	38
1941	33,054	----------	5.7	30	26	74	187
1942	2,446	----------	26.7	17	6	75	29
1943	12,456	----------	40.0	19	8	75	34

[1] Landings that were made outside the limits of the season as defined in the text were eliminated.
[2] Boats that made 2 or more landings at Coos Bay during a season were eliminated; see also footnote 1, p. 385.
[3] Boats that were in the fishery less than ½ of a season were eliminated.
[4] Boats for which no information on length could be obtained had to be eliminated.
[5] See footnote 1 on p. 385.

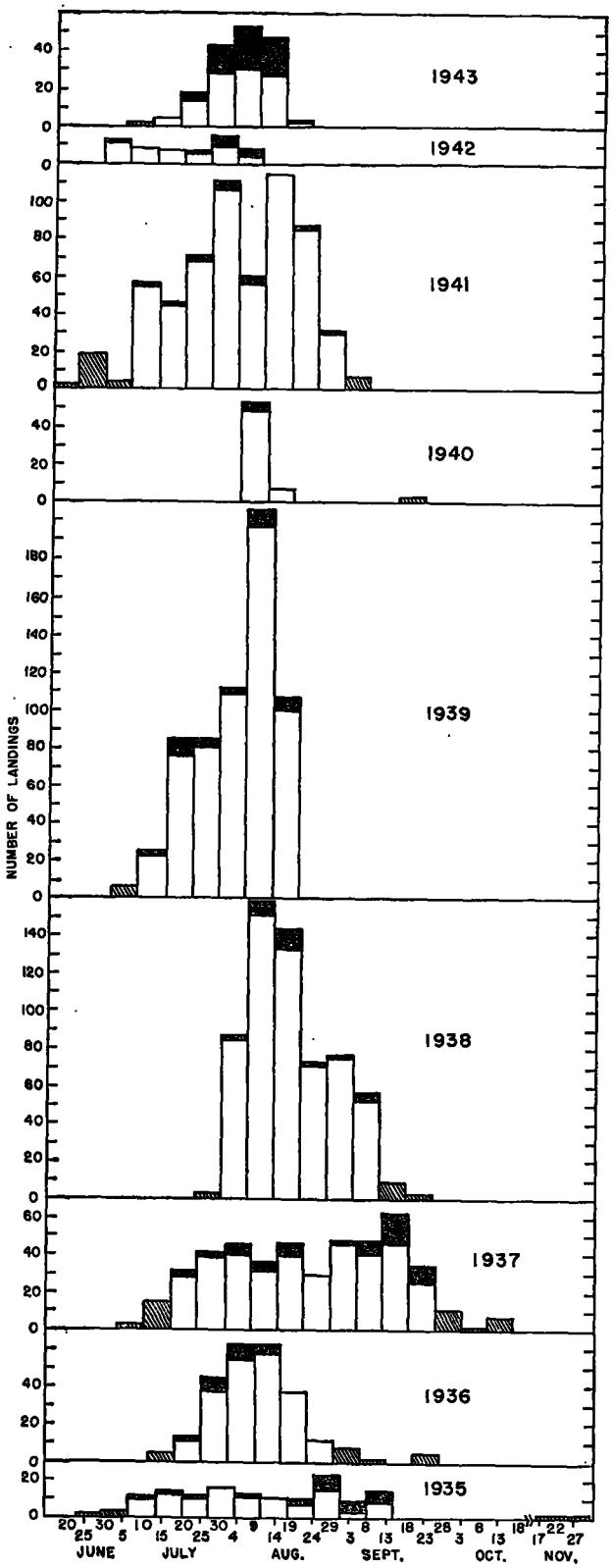

FIGURE 3.—Frequency distributions of the numbers of landings per week in each year. The hatched areas indicate landings omitted because they were outside the season as defined in the text, and the shaded areas indicate landings omitted for other reasons.

(*b*) one-third or more of the boats making landings during the week in question made only one landing (after Silliman and Clark 1945 : 54).

The effects of the applications of the preceding rules are shown in figure 3 and table 1.

After defining the seasons and the fleet involved in the fishery each season by the above rules, it is necessary to standardize the data so that the effort units are the same from year to year. The use of the device known as linkage (where the performance of a fleet in year *A* is compared with the performance of the identical fleet in year *B*, and the performance of a different fleet in year *B* is compared with the performance of that identical fleet in year *C*, and so on) would be inadvisable, since the composition of the fleet varied widely between adjacent years and the use of such a technique would result in the loss of an inordinate amount of data.

If there is a relationship between catch per unit-of-effort and boat size (or some other attribute), it is possible to compare the performance of boats of a given size rather than the performance of identical boats. This will average out the fluctuations in individual boat success due to the fishermen's skill, just as the linkage method will, and between-season comparisons will involve similar effort units.

Theoretically, it might be expected that there is a relationship of catch per unit-of-effort and boat length (as a measure of boat size). Data on boat length are available (U. S. Department of Commerce, 1935–42). For each season separately, the tons landed by each boat in each week were plotted against boat length (by 2-foot boat-length intervals) and a straight line fitted to the points by the method of least squares. The only assumption made is that the two variables are related in an approximately linear manner over the ranges of boat sizes and catch sizes occurring in these years. In all years except 1940, 1942, and 1943, the correlation is highly significant ($P<0.01$). For the three seasons mentioned, the correlations

are of doubtful, or no significance (P=@0.10). These latter values are probably due to the smaller number of boats in the fishery, the shortness of the season in these 3 years, or both (i. e., the small number of boat-weeks). Even though the slopes of these three regression lines do not vary significantly from zero, the levels of apparent abundance may still be accurately reflected by the levels of the lines.

By analysis of covariance it is possible to determine whether these nine regression lines differ significantly from the regression line of the pooled data for the nine seasons. They do, in fact, differ significantly.

Item	*Sums of squares*	*df*	*V*
Common	14, 550, 388	1, 143	-------
Separate lines (within)	12, 404, 161	1, 127	11, 006
Difference (between)	2, 146, 227	16	134, 139

The variance about the separate lines is significantly less than the variance between the separate lines; Z=1.25, P is considerably less than 0.01 (Tippett 1941: pp. 181–188). This shows that the regressions differ in slope, level, or both. The levels and slopes may be expected to vary simultaneously for two reasons. First, the smaller boats would tend to reach their capacity at relatively low levels of apparent abundance and any further rise in level of apparent abundance would not be reflected in their catch per unit-of-effort. Larger boats, however, would continue to respond through a higher range of levels of apparent abundance. Second, there is probably a minimum boat size below which, for economic and mechanical reasons, pilchard would not be caught. This is borne out by the fact that the Y-intercepts of the regression lines (using noncoded values of X) are all negative. From both of these reasons it is to be expected that the left end of the regression line would tend to be relatively fixed, while the right end would be free to move up and down in response to changes in level of apparent abundance. As a consequence, those lines at the highest level would also have the greatest slope and those lines at the lowest level would also have the least slope. Examination of figure 4 and table 2 will show that this is true for the present data.

It is thus seen that the slopes and levels of the regression lines are significantly different among the nine seasons. These differences may be interpreted as expressions of differences in levels of apparent abundance in the different seasons.

TABLE 2.—*Data on the regression of catch per week on boat length in the Oregon-Washington pilchard fishery, 1935–43*

Tons per boat-week

Season	$Y=a+bX$ [1]	Boat size, 68′–69′ [2]	Boat size, 72′–73′ [3]	Boat size, 78′–79′ [4]	r [5]	P
1935	$Y=-73+18.4X$	166	203	258	0.41	<0.01
1936	$Y=37+4.8X$	99	109	123	.27	<.01
1937	$Y=12+11.8X$	165	189	224	.25	<.01
1938	$Y=-21+10.8X$	119	141	173	.25	<.01
1939	$Y=-11+9.6X$	114	133	162	.18	<.01
1940	$Y=3+5.7X$	77	89	106	.27	@.10
1941	$Y=-12+11.5X$	138	160	195	.26	<.01
1942	$Y=-49+6.8X$	39	53	73	.26	>.10
1943	$Y=-17+14.7X$	174	203	248	.19	>.10

[1] Equation of the regression line of tons caught per week on boat length (by 2-foot boat length intervals), where Y=tons caught per week, a=Y-intercept of regression line, b=regression coefficient of Y on X, and X=boat length. Boat lengths were coded as follows: boat length class 44′–45′=1, 46′–47′=2, . . . , 88′–89′=23.
[2] Value obtained by substituting X=13 in the preceding equation.
[3] Value obtained by substituting X=15 in the preceding equation. This length was referred to as a "standard boat" in the text.
[4] Value obtained by substituting X=18 in the preceding equation.
[5] Coefficient of correlation.

A catch per standard boat-week datum may be determined, for each season, from the equation of the fitted line. It should be noted that calculating the catch per week for any particular size boat makes use of all the data going into the regressions. The numerical expression of catch per standard boat-week will depend, of course, upon the size chosen as a standard boat. For purposes of comparison with indices of abundance from other regions, the selection of a medium size is indicated, since such indices have usually been based upon the performance of a fleet of boats rather than on any standard size. (See, for example, Silliman and Clark's 1945 study of catch per unit-of-effort in California.) The modal boat-length class (72′–73′) was therefore selected as representing a standard boat. For each season the average tons per week for a standard boat were calculated from the equation of the fitted line. These values are given in table 2 and shown by the solid line in figure 5. They tend to vary around an average of slightly more than 140 tons per standard boat-week. The fluctuations around this level are rather wide and there is no significant trend during the period covered (P>0.10).

Selection of a different size boat will affect the numerical values obtained for the catch per boat-week. To illustrate this, there are given in figure 5 curves showing the catch per boat-week for the smallest boat size present in all seasons, 68′–69′ (broken line), and for the largest boat size present in all seasons, 78′–79′ (dashed line). The levels are somewhat different, but the relative changes

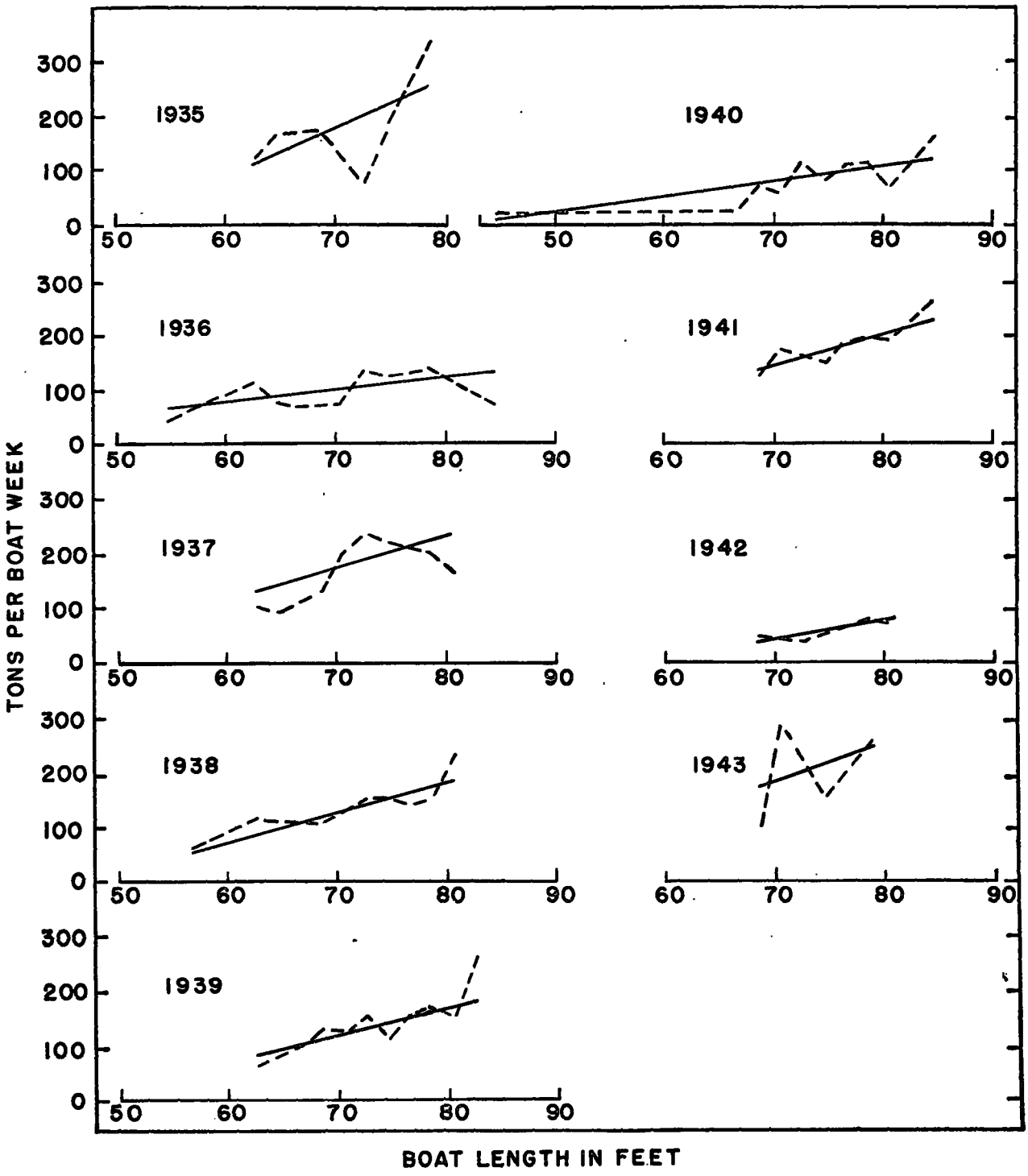

FIGURE 4.—Regression of tons landed per week on boat-length (by 2-foot boat-length intervals) for each season. The solid line was fitted by the method of least squares. The average values, for each length interval, of the points to which the solid lines are fitted are connected by the dashed line.

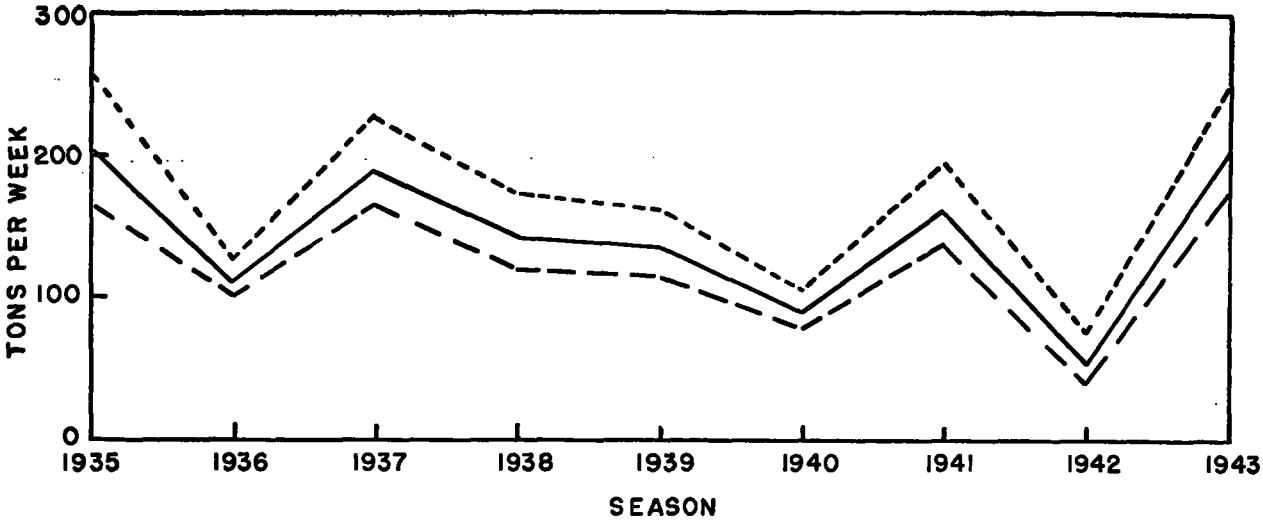

FIGURE 5.—Tons of pilchards caught per boat-week in the Oregon-Washington fishery. The broken line is based on boat-size 68′–69′; the solid line on boat-size 72′–73′; and the dashed line on boat-size 78′–79′.

are similar in all three curves. However, in contrast to the curve representing the standard boat, the curve representing the smaller boat minimizes the fluctuations, while the curve representing the larger boat accentuates them. Since boats of larger sizes are freer to respond to changes in level of apparent abundance, the dashed line in figure 5 more accurately reflects these changes than do the other two lines, although in the present instance the differences are not great. The values plotted in these lines are given in table 2.

As mentioned previously, changes in the magnitude of catch per unit-of-effort indices may be brought about by changes in the amount of effort expended, as well as by changes in apparent abundance. The former will not occur, presumably, when the intensity of the fishery is low relative to the size of the stock of fish. Records have not been kept on the number of effort units in the Oregon-Washington pilchard fishery from season to season. However, an estimate of the number of effort units in a particular season may be obtained by dividing the total catch by the catch per unit-of-effort. Comparison of the number of effort units with the catch per unit-of-effort in each season shows that, over the nine seasons covered, there is no significant correlation ($r=0.11$).

In brief, use is made of a linear relationship between average tons caught per week and boat length to obtain a catch per standard boat-week datum for each season. These data are interpreted as reflecting levels of apparent abundance; they apparently do not reflect changes in intensity. It is the variation in these levels from season to season which is of interest. No trend is apparent over the nine seasons covered; the values tend to vary around an average of slightly more than 140 tons per standard boat-week. Catch per boat-week data for larger boats more accurately reflect changes in level of apparent abundance than do data based on smaller boats.

AVAILABILITY

As indicated, these data are affected by the availability of the fish to the fishermen as well as by the actual abundance of the fish. It is known, on the basis of circumstantial evidence from size-composition of the catch and other information (summary of references in Clark 1935) and direct evidence from tagging (Clark and Janssen 1945: 41), that there is an exchange, in both directions, of fish between the northern and southern fishing grounds. A spawning area of this species is known to lie off southern California south of Pt. Conception (E. C. Scofield 1934; Ahlstrom 1948). More northern waters have not been adequately surveyed and their importance as spawning areas is unknown. It is known that important spawning took place in them in 1939 (Walford and Mosher 1941; Hart 1943). If information were available that would permit the removal of the effects of varying availability from measures of abundance in the Oregon-Washington fishery and in the California fishery, it would be possible to examine the relationship of abundance in Oregon-Washington with abundance in California.

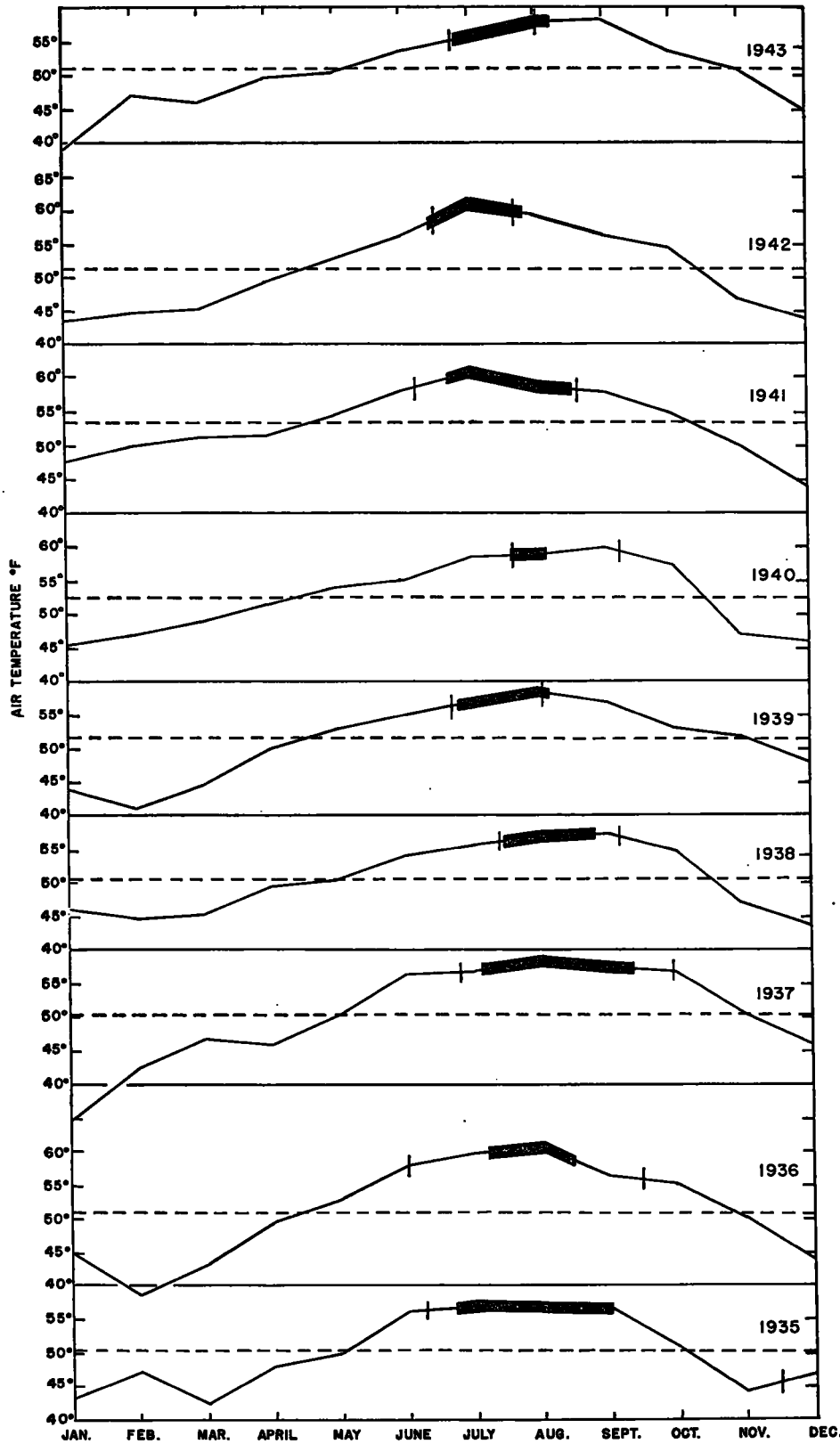

FIGURE 6.—Average monthly air temperatures, ° F., at North Head, Wash., for the years 1935–43. Vertical lines indicate the dates of the first and last landings in each year, and the solid bars the time and duration of the seasons as defined in the text. Horizontal broken lines indicate average annual air temperatures.

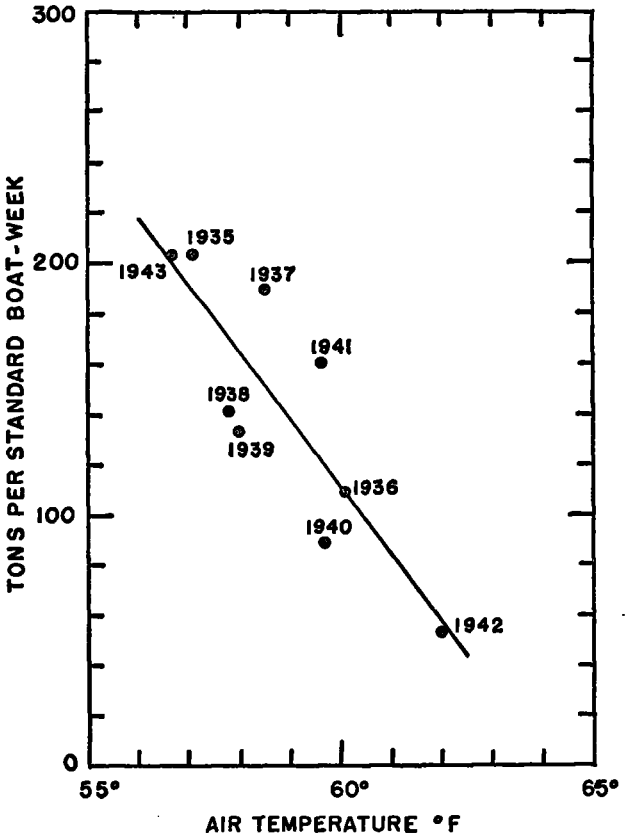

FIGURE 7.—Correlation diagram showing the relation of tons caught per standard boat-week with average daily air temperatures, ° F., during each season (as defined in the text) at North Head, Wash.

In this connection, figures 6 and 7 are of interest. In figure 6 there are shown for each year, 1935–43, the average monthly air temperatures in ° F. at North Head, Wash. (U. S. Weather Bureau, 1935–43). (Air temperatures at a land station are used in place of appropriate water temperatures, as the latter are not available.) The vertical lines indicate the dates of the first and last landings each year and the solid bars indicate the duration of the season as limited in this study. The period of the fishery in each year seems to be associated with the period of highest temperatures. To examine this seeming relationship more critically, the regression of the time of the pilchard season each year on the time of the highest weekly average of daily air temperatures in ° F., at North Head, was determined. The time of the season was expressed in terms of the number of days after June 30 on which the mid-date of the season fell. The time of the period of highest temperatures was expressed in terms of the number of days after June 30 on which the mid-date of the week having the highest average daily temperature fell. The coefficient of correlation was found to be 0.58; $P=0.10$. By commonly accepted standards, a probability value in this range neither substantiates nor invalidates the hypothesis that there is a correlation between the time of highest temperatures and the time of the fishery. This is especially true when the crudity of the methods employed is taken into consideration. Judgment must therefore be reserved for the present.

In figure 7 are shown the tons per standard boat-week plotted against the average daily air temperatures during the season at North Head, Wash. The line was fitted by the method of least squares. For this regression, the correlation is negative ($r=-0.80$) and highly significant ($P=0.01$). If the tons per boat-week data for the larger boats are used, the coefficient of correlation has the same value; the slope of the fitted line is increased. If the regression of tons per standard boat-week on average daily air temperatures during the months of July and August is considered, the coefficient of correlation is found to be -0.75 ($P=0.02$). The best catches per standard boat-week tended to be made in the seasons of lowest average daily temperatures and, conversely, the lowest catches per standard boat-week tended to be made in the seasons of highest average daily temperatures. In other words, it has been demonstrated that the return per unit-of-effort expended in the Oregon-Washington pilchard fishery, 1935–43, has been considerably influenced by an environmental condition or conditions. Of course, the effects of water temperature (as reflected by air temperature) on the habits and life history of the pilchard are unknown. These effects might be direct or they might be the result of the effects of some unknown factor upon both water temperature and the fish. Conceivably, the effect could be on the habits of the fishermen rather than upon the habits of the fish. The subject is introduced here to emphasize the need for studies of the biology of this species.

SUMMARY

1. Boat-catch data covering the years 1935–43 in the Oregon-Washington pilchard fishery are used. The relationship between boat length and tons caught per week is used to obtain catch per standard boat-week data.

2. The catches per standard boat-week showed no significant trend over the nine seasons and varied around an average of slightly more than 140 tons per boat-week.

3. It is pointed out that catch per standard boat-week is a measure of apparent abundance. On the basis of present knowledge, it is impossible to separate the effects of availability from abundance and only the combined effects of the two, or apparent abundance, can be measured.

4. Two ways in which the Oregon-Washington pilchard fishery might be affected by temperature are pointed out.

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UNITED STATES DEPARTMENT OF THE INTERIOR, OSCAR L. CHAPMAN, *Secretary*
FISH AND WILDLIFE SERVICE, ALBERT M. DAY, *Director*

JUVENILE FORMS OF *NEOTHUNNUS MACROPTERUS, KATSUWONUS PELAMIS* AND *EUTHYNNUS YAITO* FROM PHILIPPINE SEAS

By CHARLES B. WADE, Aquatic Biologist

Illustrations by Pablo Bravo

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JUVENILE FORMS OF *NEOTHUNNUS MACROPTERUS, KATSUWONUS PELAMIS,* AND *EUTHYNNUS YAITO* FROM PHILIPPINE SEAS

By CHARLES B. WADE, *Aquatic Biologist*

The juvenile forms of the various species of tuna inhabiting the Pacific Ocean are but little known. Schaefer and Marr (1948a; 1948b) were the first investigators to publish definite information regarding the young of the yellowfin tuna, skipjack or striped tuna, bonito, and frigate mackerel. Their data were secured from material taken off the west coast of Central America. Marr (1948) also recorded several specimens of juvenile *Katsuwonus*, striped tuna or skipjack, from the northern Marshall Islands. In 1880 Lütken recorded two juvenile specimens considered by later authors as perhaps *Neothunnus*, yellowfin tuna: one from an unspecified location, probably the East Indies, and the other from the South China Sea. The young of several tuna-like fishes from Japanese waters were discussed in a general way by Kishinouye (1923). Other than these, there are no references available on the juveniles of these important Pacific species.

Small but representative collections of the juvenile forms of *Neothunnus macropterus*, yellowfin tuna; *Katsuwonus pelamis*, skipjack or striped tuna; and *Euthynnus yaito*, bonito, have been made by the pelagic fish-studies section of the Philippine Fishery Program of the Fish and Wildlife Service,[1] as part of its studies on these commercially important fish. The specimens were secured by night-light operations[2] and market collecting. Night lights were used at every opportunity for more than a year aboard the Program's research vessel *Spencer F. Baird* under a wide variety of enviromental conditions ranging from secluded bays to the high seas. In addition to the use of the night light, the public markets were searched for small, tuna-like fishes. Two genera, *Euthynnus* and *Auxis*, were found principally in the markets, and *Neothunnus* and *Katsuwonus* were taken only by night light.

[1] A part of the Philippine Rehabilitation Program authorized by the Philippine Rehabilitation Act of 1946, title 50, App. U. S. Code, Sec. 1789.

[2] At night, while the vessel is lying at anchor or hove to on a hydrographic station, an electric light is suspended beneath the surface of the water and the fishes and other organisms attracted by it are collected with dip nets.

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Counts were made of the vertebrae of one or two specimens of each species. These specimens were cleared and stained in alizarin red S using Hollister's (1934) method of preparing the material. The fork length, which is measured from the tip of the snout to the end of the median caudal rays, is used as the length of the specimens throughout this paper.

NEOTHUNNUS MACROPTERUS (TEMMINCK AND SCHLEGEL)

Eighteen juvenile tuna, assigned to *Neothunnus macropterus*, were collected by the biologists of the Philippine Fishery Program aboard the research vessel *Spencer F. Baird.* They are identical with the specimens described as *N. macropterus* by Schaefer and Marr (1948a), and there is only a remote possibility that they could be the juvenile form of another species or an unknown form. These specimens were taken by dip net under a night light and from the following localities: 5 specimens, 14 to 20 millimeters fork length, Minis Island, Pilas Island Group, Sulu Archipelago, 6°37.2′ N., 121°31′ E., May 7, 1948; 13 specimens, 9.8 to 35 mm. fork length, Davao Gulf, Mindanao, 6°44.5′ N., 125°36.7′ E., May 13, 1948.

The species can be roughly identified in the field by the entirely black first dorsal and by the relatively deep, heavy body. Figures 1 through 5 show these characters at several stages of growth. The second dorsal remains colorless until the fish reaches a length of about 25 mm. At this stage the basal half of the fin develops a light brown pigmentation which becomes progressively darker as the fish grows larger.

The smallest specimen in the collection (9.8 mm.) is colorless except for an entirely black first dorsal and, just anterior to the nape, a dark brown subcutaneous area of pigment on the dorsal aspect of the head that also covers the brain. The body is lightly pigmented anteriorly and dorsally at about

15 mm., the color lighter on the sides. The head remains colorless, except for the subcutaneous area of pigment covering the brain and a few pigment spots at the tip of the snout. As the size increases, the nape, operculum, and posterior edge of the orbit become pigmented and darker. The body color becomes more pronounced and expands posteriorly as the fish grows larger, finally covering most of the dorsal and lateral surfaces to the midline of the sides. A horizontal stripe of darker pigment extends backward along the midline of the side, and is separated from the brown dorsal area by a narrow band of lighter pigmentation. In specimens of about 28 mm. there are traces of several dark, wide, vertical bars beginning to develop. These extend downward from the dorsal midline and become fainter laterally. The largest specimen in the collection (35 mm.) has 5 well-defined, dark, vertical bands.

The first dorsal had 14 spines in all specimens examined. The first spine in the smaller specimens is slightly longer or equal to the second, and equal to the second in the larger specimens. The last spine of the first dorsal almost reaches the base of the second dorsal. The combined count of the rays and finlets of the second dorsal is 22 or 23 (23 in three specimens), with 14 or 15 rays and 8 finlets.

There are 14 anal rays and 8 finlets present, with a combined count of 22. The finlets are completely

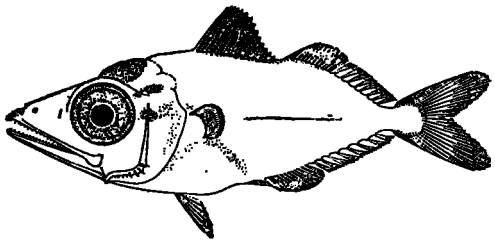

FIGURE 1.—Juvenile *Neothunnus macropterus*. Drawn from a specimen 9.4 mm. fork length.

united by interradial membranes in the smallest specimens. As the size increases, these membranes become reduced and in the largest specimens only a partial membrane connects the posterior edge of each finlet to the base of the following finlet. Pectoral rays vary from 21 in the smallest specimen to 32 in the largest, increasing in number as the fish develops.

It is difficult to distinguish between the last fin ray and the first finlet in the smaller specimens, but they are easily separated in larger specimens. The rays and the finlets differ in general appearance. Each finlet is branched distally and the branches are flattened and widely spread, which gives the outer end of the finlet a leaf-like appearance. The fin rays also are branched, but do not exhibit the flattened, spread, leaf-like appearance of the finlet. The branches of each ray remain rounded, except perhaps at the very tip where they may be slightly flattened. There is also a difference in the manner in which the rays and finlets are united to their bases. The finlets appear to set on a peduncle or base, and the basal part of the finlet almost reaches to the surface of the body. The fin rays on the other

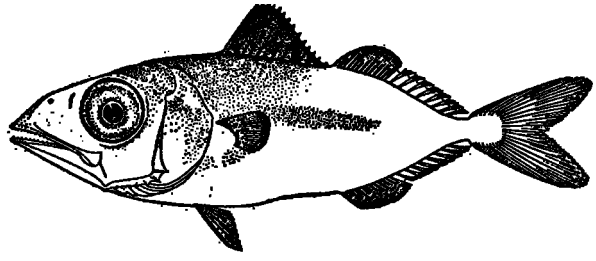

FIGURE 2.—Juvenile *Neothunnus macropterus*. Drawn from a specimen 16.5 mm. fork length.

hand, extend into the body and there is no indication of the union of the ray with its base.

There are 28 to 30 maxillary teeth on each side of the upper jaw, and 34 to 36 teeth on each side of the mandible or lower jaw. Palatine teeth are present, 12 to 14 on each side, and arranged in two irregular rows anteriorly, tapering to a single row posteriorly. Vomerine teeth are present.

The gill rakers in specimens of 16 mm. are merely minute projections, with a count of 3+1+11. In specimens of about 25 mm. fork length the count is 5+1+18 and in the largest example it is 7+1+20. The gill-raker count of adult *N. macropterus* is 7–9+1+19–22. Three large spines are present at the angle of the preoperculum in the smallest specimen. There are also two smaller spines along the vertical edge of the preoperculum and three along the lower horizontal edge. As the fish grows larger these spines become embedded in the developing preopercular bone and finally disappear. The largest specimen in the collection has only the tips of the spines at the preopercular angle still protruding from the edge of the bony deposit. When viewed by transmitted light the rest of the spines can be faintly seen embedded in the preopercular bone. The anterior portion of the lateral line is barely visible above the pectoral fin and has the

usual abrupt arch characteristic of the family Thunnidae.

The intestine lies along the right side of the body cavity and in the 35 mm. specimen there is a sharp S-shaped curve, which is the beginning of the formation of the intestinal folds. The right lobe of the liver is larger than the almost equally sized center and left lobes.

Two specimens, 16.5 and 28 mm. fork length, respectively, were cleared and stained according to the method used by Hollister (1934). The total vertebral count on each specimen was 39. There were 18 precaudal and 21 caudal vertebrae. No attempt was made to study in detail the structure of the vertebral column. The first closed haemal arch could not be exactly determined, but appeared to be either on the tenth or eleventh vertebra. The number of vertebrae (18+21=39), the shape of the anterior portion of the lateral line, and the beginning of intestinal folds place these specimens in the family Thunnidae as defined by Kishinouye (1923).

It is much more difficult to make the generic and specific determinations, and these cannot be settled with certainty until a complete collection of the juveniles of all the species of Thunnidae occurring in the Philippines has been made. Five species of this family have been recorded from Philippine waters: *Thunnus orientalis*, *Thunnus germo*, *Parathunnus mebachi*, *Kishinouella tonggol*, and *Neothunnus macropterus*. The first three species are rarely taken in Philippine waters, the fourth is common, and the fifth, abundant. An unidentified species of tuna has been reported from southern Mindanao by Domantay (1940), but no further information is available. No unknown species have been seen or collected by the biologists of the Philippine Fishery Program.

The black tuna, *T. orientalis*, is closely related or perhaps identical with the bluefin tuna, *T. thynnus*, of the west coast of North America and the Atlantic Ocean, but no effort has been made here to clarify its systematic position. The only records of this species from the Philippines were made by Dr. Albert W. Herre[3] between 1925 and 1940. Either it was observed by him or reported to him that this species was present in the Gulf of Davao, off the southeastern coast of Mindanao, and in the South China Sea off Lubang Island. As none has been seen or reported in almost two years' field work by biologists of the Philippine Fishery Program, *orientalis* is evidently extremely rare. Prior to World War II the Japanese carried on a long-line fishery for this species between Formosa and northern Luzon in the late winter and early spring months. The fish caught were large (100 to 450 pounds), and taken in depths of 25 to 30 fathoms. It seems probable that the Philippine records were also taken from deep water, as the Japanese carried on a small long-line fishery in the Davao Gulf and southeastern Mindanao prior to the war, and they also fished for tuna by deep hand lines around Lubang Island. Herre gives no indication of the abundance of this species, but it is assumed that it is extremely rare, as no other records are available.

Kishinouye (1923) reported the range of water temperatures inhabited by *T. orientalis* to be 5° to 20° C. and the optimum temperature from 10° to 15° C. Water temperatures recorded by the oceanographic studies of the Philippine Fishery Program in the Gulf of Davao and southeastern Mindanao are 27° C. on the surface and at 50 meters; 15° C. at 200 meters; and 10° C. at 350 meters. The temperature of the ocean is somewhat lower off Lubang

[3]Unpublished manuscript, Check List of Philippine Fishes.

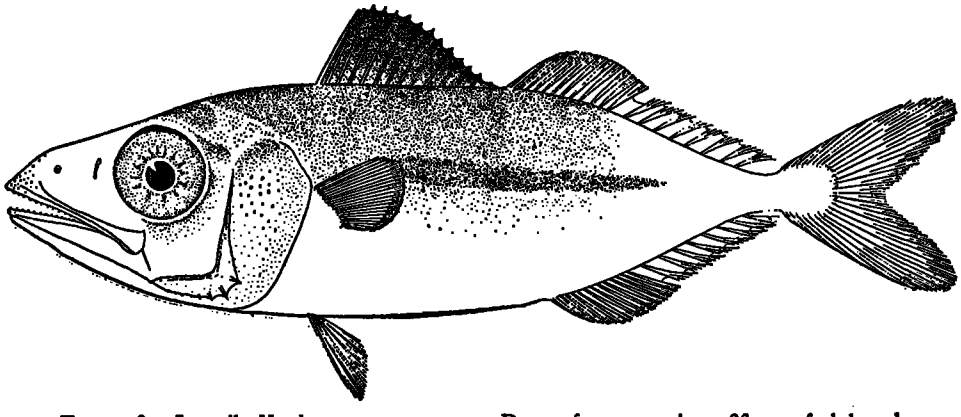

FIGURE 3.—Juvenile *Neothunnus macropterus*. Drawn from a specimen 23 mm. fork length.

Island, being 22° C. at 50 meters; 15° C. at 175 meters; and 10° C. at 375 meters. A further decline is recorded from northern Luzon where the temperature is 21° C. at 50 meters; 15° C. at 150 to 175 meters; and 10° C. at 350 meters. In the Sulu Sea the temperature is 28° to 30° C. at 50 meters; 15° C. at 200 meters; and 10° C. at 800 meters. If Kishinouye's observations regarding the range of temperature for this species are significant, it seems probable that the northern Philippines represent the southern limit of the regular range of black tuna, and the other records are of fish that have strayed beyond their normal habitat.

Kishinouye (1923) was of the opinion that *T. orientalis* spawns in Japanese offshore waters, as he found black tuna with greatly enlarged gonads there during June and July, and spent gonads in August. Inasmuch as most Philippine waters have temperatures above the indicated range for this species and as there are indications that it spawns in more northern waters, in all probability the juveniles found in Philippine waters would not be *orientalis*.

The albacore, *Thunnus germo*, has been reported from the Philippines by Seale (1908), Villadolid (1937), and Herre (in manuscript). In 1937 a single specimen was identified and sent to the Philippine Bureau of Science by Agustin F. Umali, of the Philippine Bureau of Fisheries, where the identification was confirmed by the museum authorities. This specimen was destroyed during the liberation of Manila in 1945. Umali reports that there were six albacore in the public market at Naga, Luzon, where he secured the specimen and that they were caught by hand line in 100 to 120 fathoms of water. This species seems of irregular occurrence in Philippine waters, as there are no indications of its capture by prewar Japanese long-line fishermen in or near the Philippines, although it was caught commercially in small numbers in the former Japanese-mandated islands. The range of water temperature for albacore was reported by Kishinouye (1923) to be 10° to 25° C., which is at, or largely below, the temperature range of most Philippine waters. No information is available as to the location or time of spawning, but this species is believed to spawn in the open ocean. In view of its extreme rarity and the fact that it seems to be almost entirely oceanic in habit, young tuna found in Philippine waters most likely do not belong to this species.

There is a single record of the big-eyed tuna, *Parathunnus mebachi*, from the Philippines. This was made by Domantay and Herre in 1940 from the Sulu Sea, near Zamboanga, Mindanao, and recorded by the latter in his Check List of Philippine Fishes. The apparent scarcity of this tuna would make doubtful the presence of juvenile fish of this species in Philippine waters. Also, the 9 dorsal and anal finlets of the big-eyed tuna further separate the specimens at hand from it.

The least tuna, *Kishinouella tonggol*, is commonly found in Philippine waters at certain seasons although seemingly not nearly so abundant as the yellowfin. It is the only other species of Thunnidae in these waters the juveniles of which are likely to be represented in the collections of the Philippine Fishery Program, as specimens approaching maturity have been taken by trolling from the *Spencer F. Baird*. However, the gill-raker count of 5–6+1+16–17 for adult *K. tonggol* would eliminate it inasmuch as the larger juveniles of *N. macropterus* already have a greater number of gill rakers than is present in the adult least tuna. This evidence,

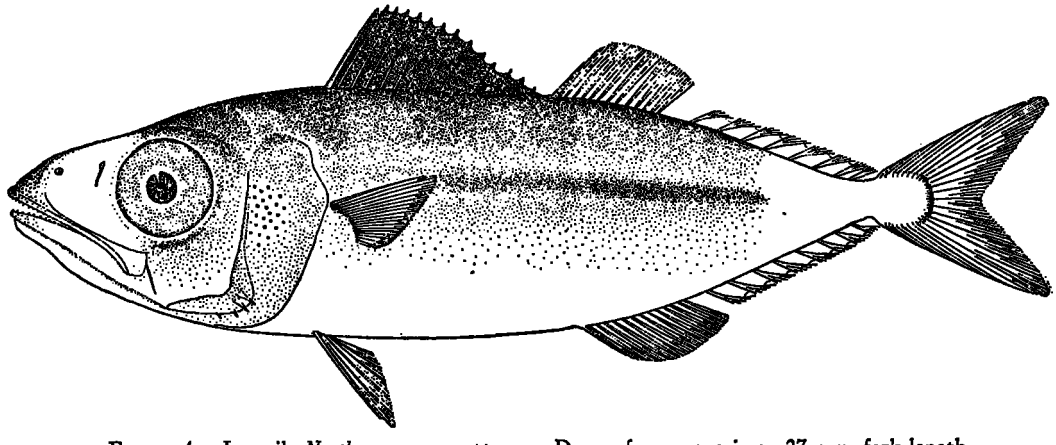

FIGURE 4.—Juvenile *Neothunnus macropterus*. Drawn from a specimen 27 mm. fork length.

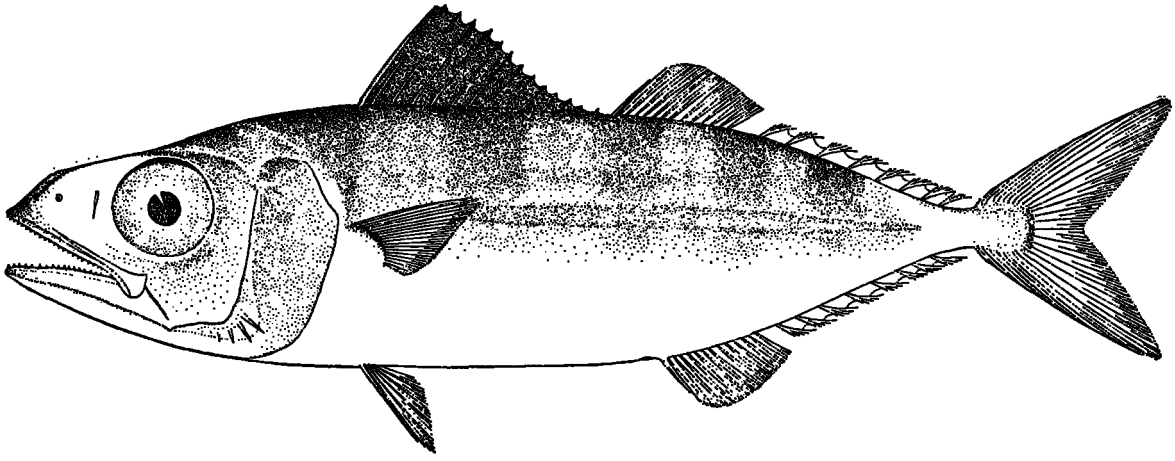

FIGURE 5.—Juvenile *Neothunnus macropterus*. Drawn from a specimen 37.5 mm. fork length.

although slight, seems to eliminate the possibility that the juvenile specimens in the collections which have been assigned to *N. macropterus* could be *K. tonggol.*

KATSUWONUS PELAMIS (LINNAEUS)

Six specimens, identified as *Katsuwonus pelamis*, were taken in the following locality: 6 specimens, 13 to 27 mm. fork length, Minis Island, Pilas Island Group, Sulu Archipelago, 6°37.2′ N., 121°31′ E., May 7, 1948, night light, *Spencer F. Baird.* These specimens agree with the description of *K. pelamis* as given by Schaefer and Marr (1948a) for the juvenile forms from the west coast of Central America.

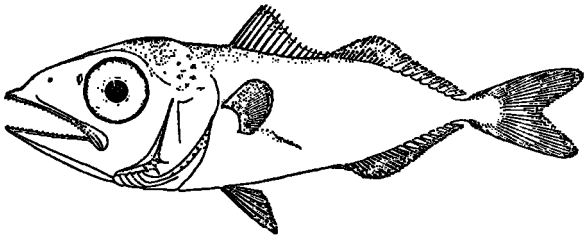

FIGURE 6.—Juvenile *Katsuwonus pelamis*. Drawn from a specimen 13 mm. fork length.

The 13 mm. specimen (fig. 6) is almost entirely colorless, the light brown color being confined to the anterior portion of the dorsal surface of the body and to the brown subcutaneous pigmentation covering the brain. There is a slight trace of color on the distal portion of the first dorsal. The largest specimen illustrated in figure 9 is lightly and evenly pigmented over the entire dorsal aspect of the body. Laterally, the color becomes lighter then abruptly darkens, forming a dark longitudinal band along the midline of the sides. The nape, operculum, and posterior margin of orbit are light brown. The tip of the snout, maxillary, and anterior half of the mandible are lightly pigmented. The first dorsal is irregularly patterned distally with light brown, but is colorless on the basal half. No traces of

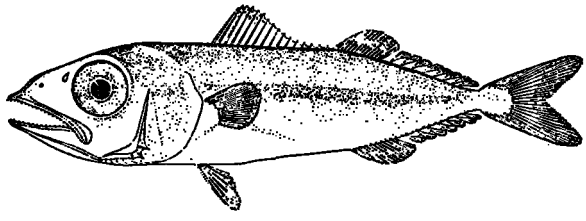

FIGURE 7.—Juvenile *Katsuwonus pelamis*. Drawn from a specimen 18 mm. fork length.

darker vertical bars are present in any of the available specimens.

There are two large spines at the angle of the preoperculum. In the smallest specimen there are, in addition, three small spines along the vertical edge of the preoperculum, and four along the ventral edge. As the fish increases in size bone is deposited between these spines which gradually disappear. In the largest specimen only the tips of the two large spines are plainly visible, but traces of additional spines can be seen when viewed by transmitted light.

The first dorsal has 16 spines, and the last spine almost reaches the base of the second dorsal. There is a total count of 22 or 23 (22 in one specimen) second dorsal rays and finlets. Although difficult to count accurately in the smaller specimens, there are 15 rays and 7 or 8 finlets (7 in one specimen).

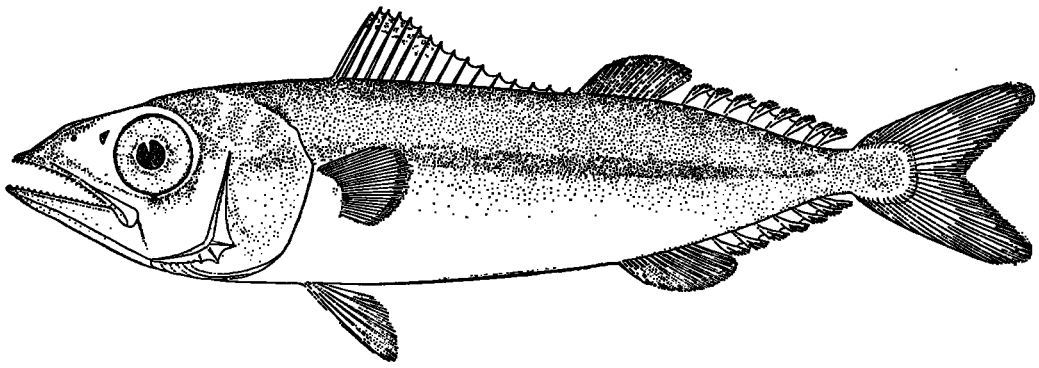

FIGURE 8.—Juvenile *Katsuwonus pelamis.* Drawn from a specimen 24 mm. fork length.

The dorsal finlets are united by interradial membranes in the smaller fish. This membrane is reduced as the fish grows larger, and in the largest specimen the membrane joins the posterior outer edge of each finlet with the base of the following finlet. The total count of anal rays and finlets is 21 or 22 (mostly 22). A single specimen has 14 rays and 7 finlets and the rest have 15 rays and 7 finlets. The number of pectoral rays varies according to the size of the specimen and no count was made.

On the largest specimen the gill-raker count is 2+1+22. Only small projections are developed on the upper angle of the gill arch and the ventral one-third of the lower angle has not as yet developed gill rakers. Gill rakers were not counted on the smaller specimens. Maxillary teeth are about 21 on each side of the upper jaw; and mandibular teeth, about 26 on each side of the lower jaw. Palatine teeth are present and about 8 in number. Vomerine teeth are absent.

The vertebrae were counted in the 27 mm. specimen which was cleared and stained with alizarin red S. There were 20 precaudal and 21 caudal vertebrae for a total of 41. The "trellis" of Kishinouye (1923) was beginning to form although not completely unified. The first closed haemal arch was on the twelfth vertebra.

The structure of the vertebral column identifies these specimens with the family Katsuwonidae as described by Kishinouye and the vertebral count of 20+21 identifies them as *Katsuwonus pelamis.* The specimens also agree in other characters with the description of this species as given by Schaefer and Marr (1948a).

EUTHYNNUS YAITO (KISHINOUYE)

Thirty-eight of the 40 juvenile specimens identified as *Euthynnus yaito* were found in the public markets of Batangas, Batangas Province, Luzon; Taal, Batangas Province, Luzon; and Manado, Celebes, Netherlands East Indies. The remaining two specimens were taken under a night light aboard the research vessel *Spencer F. Baird.*

Specimens were taken from the following localities: 2 specimens, 33.5 and 35 mm. fork length, Marigabato Point, Cotabato Province, Mindanao, 7°2′ N., 124°12′ E., May 11, 1948, night light, *Spencer F. Baird;* 1 specimen, 115 mm. fork length, Manado

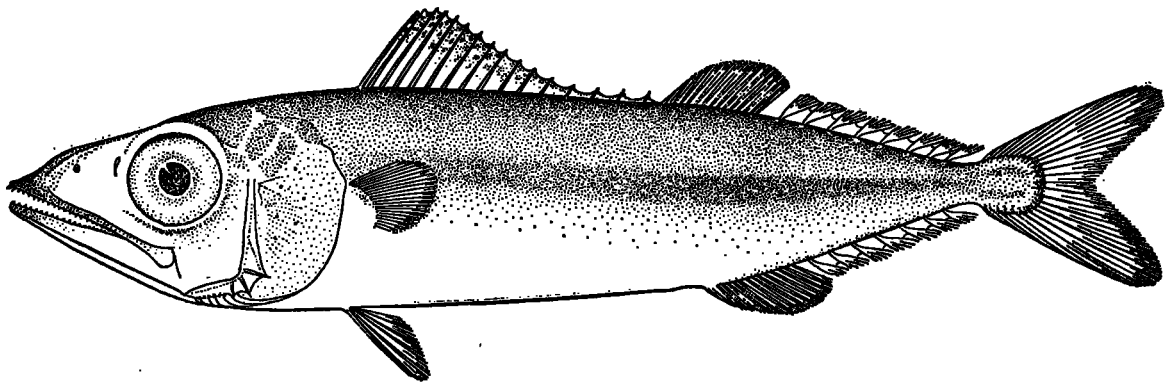

FIGURE 9.—Juvenile *Katsuwonus pelamis.* Drawn from a specimen 27 mm. fork length.

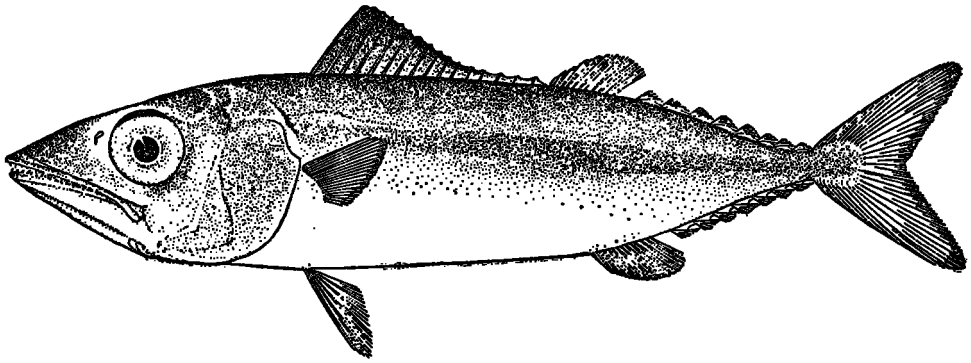

FIGURE 10.—Juvenile *Euthynnus yaito*. Drawn from a specimen 33.5 mm. fork length.

Public Market, Manado, Celebes, Netherlands East Indies, March 6, 1948; 7 specimens, 143 to 178 mm. fork length, Batangas Market, Batangas, Luzon, April 20, 1948; 4 specimens, 127 to 175 mm. fork length, Taal, Batangas Province, Luzon, May 10, 1948; 2 specimens, 40 and 44 mm. fork length, Batangas Market, Batangas, Luzon, May 17, 1948; 2 specimens, 40 and 68.4 mm. fork length, Batangas Market, Batangas, Luzon, March 12, 1949; 1 specimen, 80 mm. fork length, Batangas Market, Batangas, Luzon, March 28, 1949; 1 specimen, 76.5 mm. fork length, Batangas Market, Batangas, Luzon, April 20, 1949; 18 specimens, 73 to 112 mm. fork length, Batangas Market, Batangas, Luzon, April 25, 1949; 2 specimens, 117.5 and 131 mm. fork length, Batangas Market, Batangas, Luzon, April 27, 1949.

The body of small specimens is light brown dorsally (fig. 10), becomes paler laterally toward the midline of the side, and a dark longitudinal band occurs along the midline of the side. The body is pale ventrally and the pigmentation extends only slightly below the midline of the sides. The first dorsal is uniformly dark brown for the first three or four anterior spines. On the remaining spines the dark color is confined to the distal margin of the fin and approaches the base only near the posterior spine. Basally, the rest of the fin varies from almost entirely colorless to a light brown. The first dorsal is never uniformly colored and the other fins are colorless. The head is lightly colored with dark areas on the nape, operculum, and anterior half of the snout. There is a conspicuous crescent-shaped, light area behind the eye.

The body color and the head darken as the fish grows larger, as shown in figures 10 to 13. From 9 to 13 darker vertical bars begin to develop dorsally on the body at about 60 mm. fork length. These bars extend downward on the sides, becoming lighter laterally. In some specimens they reach only to the midline of the sides, while in others they extend well below the midline. These vertical bars are present on the largest specimens (68 to 178 mm.) in the collection. The head becomes almost uniformly dark except for a light area posterior to the eye. The first dorsal retains the color pattern of the smaller specimens. The anterior spines and the tips of the posterior spines are dark brown, and the basal part of the fin is lighter in color. The second dorsal is lightly pigmented on the basal half of the fin at

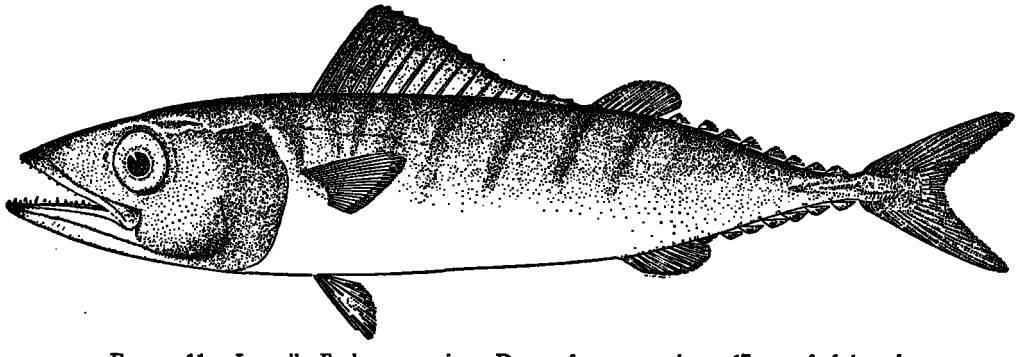

FIGURE 11.—Juvenile *Euthynnus yaito*. Drawn from a specimen 67 mm. fork length.

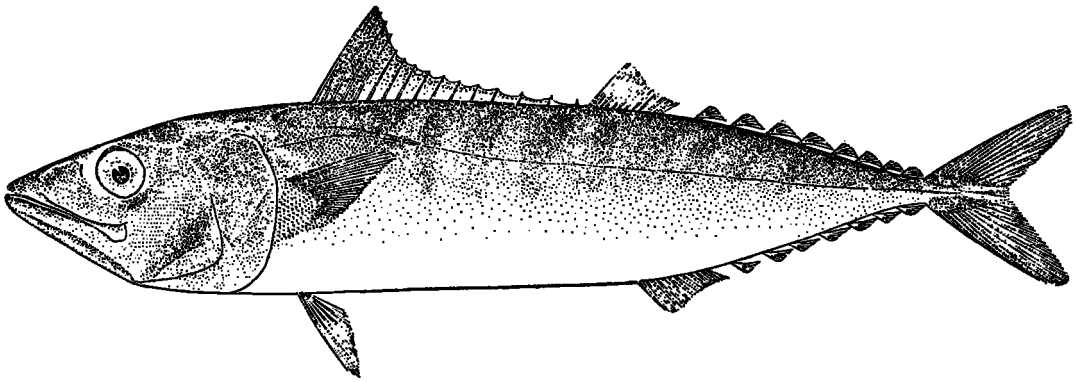

FIGURE 12.—Juvenile *Euthynnus yaito*. Drawn from a specimen 110 mm. fork length.

about 70 mm. and becomes slightly darker as the fish grows larger. Pectoral and caudal fins are progressively more pigmented as the size increases. The remaining fins are colorless.

There are 16 spines in the first dorsal and the posterior spine almost reaches the base of the second dorsal. The second dorsal has 12 to 14 rays (mostly 13) and 8 finlets. The anal fin has 13 or 14 rays (13 in one specimen) and 7 anal finlets. In the smallest specimens the interradial membrane partly connects the finlets. This connecting membrane has almost disappeared by the time the fish is 70 mm. in length, and is absent in the large specimens.

The gill rakers are small and difficult to count in the smaller specimens, and the full complement has not yet developed. The gill-raker count on a 35 mm. specimen was 4+1+20, increasing to 7–8+1+22–23 in specimens of 127 to 175 mm.

A vertebral count was made on a 44 mm. specimen which was cleared and stained in alizarin red S. The vertebrae totaled 39, with 20 precaudal and 19 caudal. The first closed haemal arch was either on the 15th or 16th vertebra, but its exact position could not be determined without dissection, which was not desirable. It appeared either to be closed or the ends of the haemal spines were lying close together on the 15th vertebra, but the haemal arch on the 16th vertebra was definitely closed. Inferior foramina are present on the posterior precaudal and about 10 anterior caudal vertebrae. The lateral processes of the posterior caudal vertebrae were beginning to develop.

The maxillary and mandible have about 35 small, pointed teeth in a single row on each side of the upper and lower jaws. Palatine teeth are present in a single row of 11 to 13 small, pointed teeth. Vomerine teeth, 4 or 5 in number, are small and easily overlooked. In the two smallest specimens there are traces of two spines at the angle of the preoperculum. In the larger specimens bone has completely covered the spines which can no longer be seen.

The intestine lies along the right side of the abdominal cavity, and is fairly straight and not

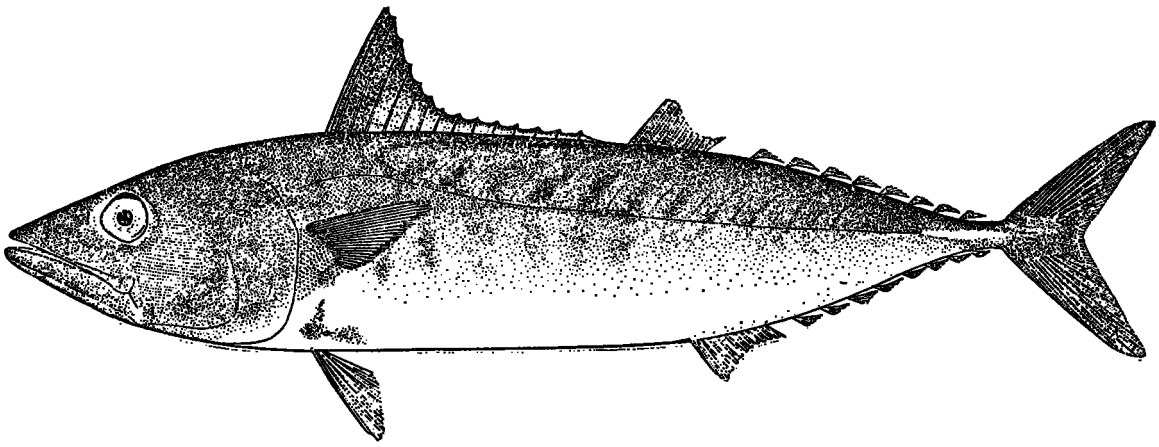

FIGURE 13.—Juvenile *Euthynnus yaito*. Drawn from a specimen 156 mm. fork length.

folded. The liver has three lobes of which the right lobe is by far the longest.

These specimens have the number of vertebrae and the complex vertebral structure called a "trellis" which are characteristic of the Katsuwonidae as defined by Kishinouye (1923). Within this family the elongated right lobe of the liver and the posterior position of the first closed haemal arch correspond to previous descriptions of the genus *Euthynnus* (Kishinouye 1923; Schaefer and Marr 1948b), in which these specimens are placed.

Kishinouye (1919) described a second species, *Euthynnus lineatus*, from Manzanillo, Mexico. His description was based upon a single specimen, which was separated from *E. yaito* mainly by its coloration and the size of the head. The juvenile forms of *E. lineatus* have recently been described by Schaefer and Marr (1948b). Comparison of their description with the present specimens shows several consistent differences, principally in the vertebral and gill-raker counts, color pattern, and the slightly greater number of dorsal spines and rays and anal rays in *E. yaito*.

There are usually 37 vertebrae in *E. lineatus*, although occasionally there may be 39. Juvenile *E. yaito* from the Philippines had a vertebral count of 39 in the specimens examined. Too little material of both species has been studied to define accurately the vertebral count, but there seems consistently to be a difference of two vertebrae in the two species.

There are fewer gill rakers on the first gill arch of *E. yaito* than on that of *E. lineatus*. Philippine specimens of *yaito* have a total count of 31 or 32 gill rakers, and *lineatus* about 38. The gill rakers of 35 adult *E. yaito* were counted and they varied from 29 to 33 (mostly 30 to 31), which is the same as in the larger juveniles.

There were 16 spines in the first dorsal of the specimens of *E. yaito* examined; 15 and occasionally 14 have been described for *E. lineatus*. According to Kishinouye (1923) the first dorsal of *yaito* has 15 to 16 spines, but no juvenile specimens were found with 15 spines in the present study. There are 13 rays in the second dorsal of the Philippine specimens instead of the 12 present in *lineatus*. Kishinouye gave the second dorsal ray count as 12 to 13 for *yaito*, but again none was found with 12 rays in these investigations. The anal rays of *yaito* numbered 14, rarely 13 as compared with the 11 or 12 of *lineatus*. Thirteen was the number of anal rays given for *yaito* by Kishinouye. The dorsal and anal fin ray counts of *E. yaito* were generally at the upper limits of the counts given by Kishinouye for this species. Statistical treatment of a large series of both species may show significant differences in fin ray counts.

There are certain differences between the color patterns of the two species that seem characteristic. Schaefer and Marr (1948b) reported that the entire first dorsal of *E. lineatus* was heavily pigmented in all specimens studied by them. In Philippine specimens of *E. yaito* the heavy pigment is confined to the anterior part of the fin and to the outer ends of the posterior spines; and the basal part of the remainder of the fin is either almost colorless or lighter in color than the distal. The basal half of the second dorsal is less heavily pigmented, and there is no conspicuous series of dark spots along the anal base or on the following finlets. The vertical bars are more numerous in *E. yaito* and persist until the fish reaches a larger size. There is a pronounced pale, crescent-shaped area behind the eye of *yaito* which is not evident in *lineatus*.

SPAWNING AREAS

The finding of juvenile forms of *Neothunnus macropterus*, *Katsuwonus pelamis*, and *Euthynnus yaito*, three species of tunas inhabiting Philippine waters, has determined several probable spawning areas for these fish. In addition, the juvenile forms of two species of the genus *Auxis*, previously described by Wade (1949), have been taken in the same localities and presumably spawning by those species occurs there.

Juvenile yellowfin tuna, *N. macropterus*, were collected from the Davao Gulf, Mindanao, and at Pilas Island, Sulu Archipelago, near Zamboanga, Mindanao. These two areas are some 250 to 300 miles apart. Davao Gulf is located at the southeastern corner of Mindanao, and Pilas Island is south of the tip of the Zamboanga Peninsula at the southwestern end. All specimens were secured during the first half of May 1949, and the small size of the specimens would indicate that spawning took place the preceding month.

A spawning area for the striped tuna was also established at Pilas Island, Sulu Archipelago, Mindanao. The specimens secured in that area were small and probably were spawned the month previous to their capture in May 1948.

Three spawning areas were located for *Euthynnus yaito*. A single specimen, taken from the south-

eastern part of the Celebes Sea, was found in the market at Manado, Celebes. This specimen was 115 mm. fork length and probably was three or four months old at the time of its capture in March 1948. Two small specimens were taken from the Moro Gulf at Marigabato Point, Cotabato Province, Mindanao, in May 1948. These specimens probably were spawned the month before they were captured. The greatest number of juvenile *E. yaito* were collected at Batangas, Batangas Province, Luzon, where thirty-seven specimens ranging in length from 40 to 175 mm. fork length were secured during March, April, and May of 1948 and 1949. The range in size indicates that some may have been spawned as long as six months before their capture and that the spawning season in this locality extends over a 4- to 6-month period. The specimens collected at Batangas came from the commercial fisheries of Batangas and Balayan Bays. Both of these bays are large and open, and freely accessible to the sea. It appears certain that this species spawns in or near both of these bays. The young of *E. yaito* come into the markets mixed with catches of Engraulidae, Clupeidae, and other small fishes which are caught in fish traps along the shore, or by beach seines and round haul nets.

It should be realized that the present knowledge of the several spawning areas is based primarily upon the results of exploratory operations over a large area and that additional intensive research in the future will undoubtedly extend the known spawning areas of these species. It is probable that all the southern half of Philippine waters and much of the northern half will be found to be the spawning grounds of several species of tuna.

SUMMARY

Several juvenile stages of three species of tuna living in Philippine waters were collected by means of night lights and market studies. Two species, *Neothunnus macropterus* and *Katsuwonus pelamis*, were found entirely in night light collections and the third, *Euthynnus yaito*, was taken mainly from the commercial catch of small fishes found in the public markets.

Both *Neothunnus macropterus* and *Katsuwonus pelamis* agree with Schaefer and Marr's (1948a) description of the juveniles of these species collected off the west coast of Central America. Philippine specimens of *Euthynnus yaito* differ from *E. lineatus* of the eastern Pacific and agree more closely with Kishinouye's (1923) description of *E. yaito* from Japanese waters.

On the basis of the present collection of juvenile forms, possible spawning localities for several species of tuna can be designated. Spawning areas for *N. macropterus* possibly occur in Davao Gulf, Mindanao, and at Pilas Island, Sulu Archipelago. A spawning locality was established for *Katsuwonus pelamis* at Pilas Island, Sulu Archipelago. There is evidence that the bonito, *Euthynnus yaito*, may spawn in the vicinity of Manado, Celebes, Netherlands East Indies; Marigabato Point, Cotabato Province, Mindanao; and Batangas and Balayan Bays, Luzon.

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DESCRIPTION OF A PROJECTION DEVICE FOR USE IN AGE DETERMINATION FROM FISH SCALES

By KENNETH H. MOSHER, Aquatic Biologist

Many scale reading devices of varied design have been reported by workers engaged in fishery research, however, most of those described or used have had serious disadvantages affecting the ease of operation or the accuracy of the results obtained. Consequently, it appears useful to describe in detail the instrument which has proved very satisfactory in the study of the ages of the California sardine or pilchard. The original unit was developed in 1938 and 1939 concurrently with the investigation of the readability of the sardine scales and otoliths by the Fish and Wildlife Service in California. This instrument was a major factor in the development of a successful method of determining age from the difficult markings on the scales of this species.

The original instrument has been substantially improved from time to time by the addition of certain refinements to provide a clearer image and brighter field. During the course of the sardine program, similar instruments were constructed for workers in Monterey and Terminal Island, Calif. so that at present there are three such units in use on the sardine studies, each calibrated to the same magnification.

The success achieved with this apparatus in determining the age of the sardine sugested its suitability for age determination in other species.

The instrument described in the following paragraphs was constructed by the author at the Seattle Laboratory for the Alaska Fishery Investigations for age determination of salmon and herring. It has been patterned after the one in use in the sardine investigation.

The unit consists essentially of a microscope of suitable power; a 90° prism ½ to ¾ inch long, silvered on the largest face; an 8- by 10-inch plate glass mirror; a piece of white celluloid or white paper upon which the image is projected; and a suitable light source. When a large number of scales are to be examined, it is desirable to equip the microscope with a mechanical stage in order to bring the various scales rapidly and precisely into the field of the objective.

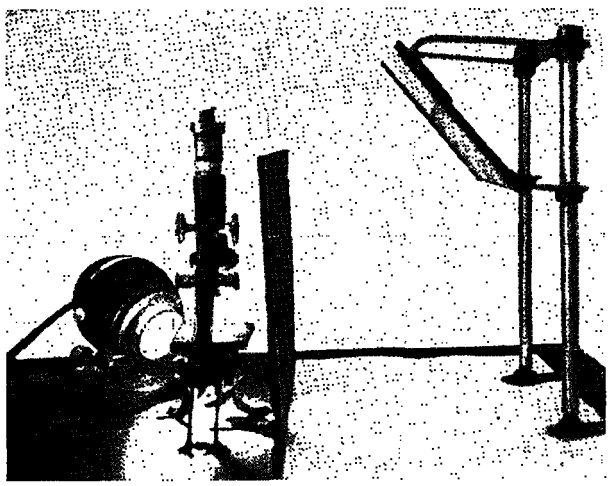

FIGURE 1.—Microprojector in operation, viewed from the operator's position. Note location of the controls of the microscope and lamp in relation to the projected image.

The proper magnification of the adult salmon scales which are approximately 4 to 8 mm. in diameter requires the use of a 40-mm. objective with a 6-power eyepiece, or equivalent. Using a 25-mm. objective with the same ocular gives a satisfactory image for use with the 1- to 3-mm. diameter scales of juvenile salmon. For larger scales such as herring and sardines, a lower power of ocular or objective, or both, will be required. The optimum magnification to use with any particular fish scale can best be determined through experiment, keeping in mind that too great a magnification tends to enlarge the details of the scale surface to the point where they obscure the annular marks and too small magnification will not reveal the annuli clearly. There is a relatively narrow range of magnifications wherein the annuli appear to the best advantage. For most scales examined, the optimum results were obtained when the projected image of the sculptured portion was around 150 mm.

Any microscope of the desired power with corrected optical parts will be adequate for this purpose. Coated optics in a double or triple nosepiece, fine adjustment, condenser, iris diaphragm, and mechanical stage will prove convenient but are not essential to satisfactory operation of the instrument. The microscope incorporated into the present unit is an old one, but the results have been very satisfactory. A good plate-glass mirror is required. A common glass mirror should not be used as the flaws will cause severe distortions which will render the unit inaccurate for measurement of the image. On the other hand, more expensive types, such as the first surface ophthalmic mirrors, have been tried with the conclusion that they are not superior to those of plate glass. The light source is one of the most important items in the projector. It must provide a bright, clear light with a flat field. The best lamps for this purpose are some of the newer types designed for microprojection.

In constructing the device, a piece of ⅝- to ¾-inch plywood, approximately 18 by 36 inches is required for the base. Two metal rods or pipes ½ to 1 inch in diameter are needed to support the mirror at the proper angle and height above the base. In the present unit this support is furnished by brass rods ⅝ by 18 inches, threaded for about 2½ inches on one end. These fit into two ⅝-inch holes drilled in the plywood base about 9 inches apart and a few inches from the right end. They are securely fastened by the use of washers and nuts.

A holder for the mirror was made from 20-gauge brass, held at the proper angle to the supports by ⅛- by 1½-inch brass straps. The mirror holder could be made of a variety of materials such as wood, plastic, or metal. The important consideration is that the mirror be held rigidly at a 45° angle to the base and at the same time be adjustable up and down on the supports in order to center the image for the height of the microscope used. In this instrument the holder is locked firmly in any desired position by means of set screws in metal collars. Once the holder is set up and adjusted for a particular microscope, it will not be necessary to change the adjustment. When the mirror has been firmly set in place, the microscope should be placed about 15 or 16 inches to the left side of the mirror. This is the most satisfactory arrangement for a right-handed person, as focusing can be done with the left hand, leaving the right hand free for the recording of data.

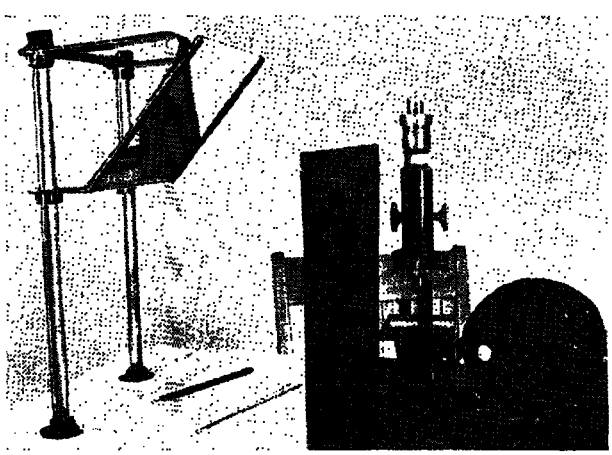

FIGURE 2.—Microprojection set-up. Illustrates the relation of parts to operator's position. Viewed from the back of the device.

A holder for the prism can be devised easily from metal tubing, wire, plastic, or other material. The prism should fit directly on the ocular of the microscope and should be attached securely so as not to shake off or become out of alignment with the microscope and mirror. The lamp is then set so as to throw its light on the microscope mirror, and the whole unit adjusted by trial and error until the projected image is clear, distinct, and properly placed for most convenient observation. When the adjustment is complete, the various instruments should be fastened in place to avoid the need for subsequent readjustment.

For best results the projector should be used in a relatively dark room. A photographic dark room is most suitable, but if this is not available, sufficient darkness can be obtained by covering the windows with heavy black curtains while using the machine. Satisfactory conditions can also be obtained by placing a cardboard or plywood box over the working area of the projector. Such a cover, as well as all other parts of the unit, should be painted a dull black to prevent reflection of light. It will also prove advantageous to place a piece of ¼-inch plywood or heavy cardboard vertically at the microscope between it and the mirror, just high enough for the prism on top of the microscope to project over it. This also should be painted a dull black on both sides to prevent stray light-rays from hitting the projected image.

If the optical items are of good quality and the adjustments are accurate, there should be very little if any distortion of the image as it is moved from one side of the field to the other.

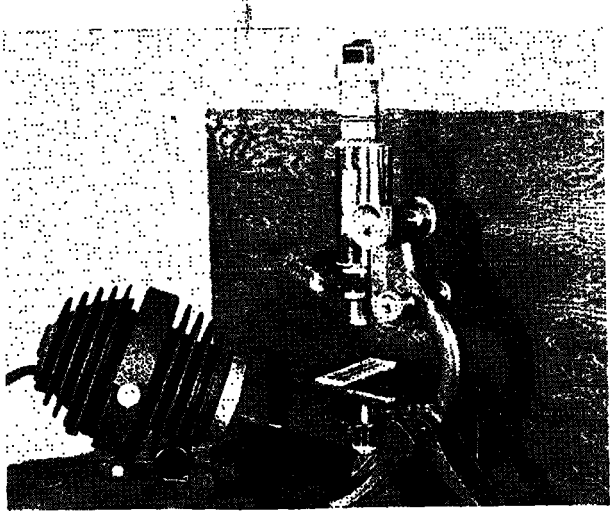

FIGURE 3.—Closeup of the microprojector, showing the relative position of the lamp, microscope, and prism. Viewed from a point to the left of the operator.

This projector can be assembled at relatively small cost, particularly if the microscope, with the necessary oculars and objectives, is on hand. The estimated cost of the prism at today's prices would be about $6 and that of the plate glass mirror about $1. The cost of miscellaneous material such as metal, plywood, washers, screws, nuts, collars, and paint is about $10; making the total outlay for accessory materials less than $20.

The advantages of this type of scale reader over the more conventional models are numerous and far outweigh the outlay of time and materials required for its construction. Advantages obtained through the use of this instrument are:

1. There is considerably less eyestrain with this unit than with direct examination of the scales through a microscope.
2. The image of the scale is clear and easily studied.
3. The image can be studied at a convenient level and in front of the operator with the controls at easy working distance.
4. The image can be measured, traced on paper, or photographed.
5. The image can be viewed by two or more workers at once which is very useful in the demonstration of scale reading, and also in arriving at proper interpretation of difficult scale markings.

The projection of the scale image provides objectivity in scale reading not ordinarily possible. Permanent records of all scales examined can be obtained by marking the base of the scale, the annuli, the margin, or other desired features on paper. These records can be used for the computation of lengths of fish at various ages, determination of growth rates, and for other purposes.

To facilitate statistical analysis it is suggested that punch cards containing a millimeter scale printed along one edge be used for recording the scale features. The "zero" mark of the ruler is placed at the base of the sculptured portion of the scale, or at the center of the nucleus, depending on the type of scale under study, and the annuli, scars, margin of the scale, and other data indicated by appropriate marks along the ruler. Data on time and locality of capture, sex, age, year class, etc., can be punched on the cards if desired. The data recorded on the cards will permit studies of such problems as racial composition, variations due to environmental factors, variations between year classes, and variations between readers, without further examination of the scales.

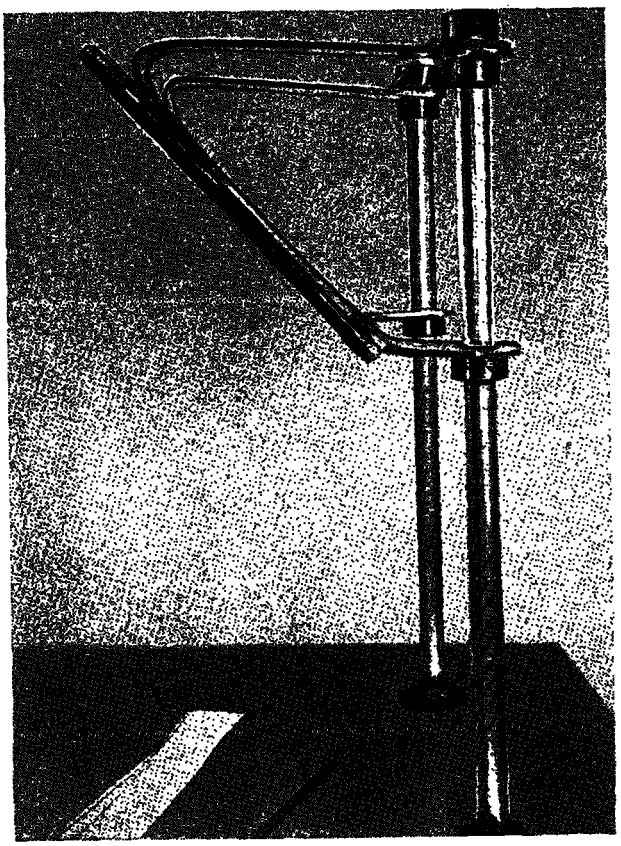

FIGURE 4.—Closeup of mirror and holder.

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OBSERVATIONS ON THE SPAWNING OF PHILIPPINE TUNA

By CHARLES B. WADE, Aquatic Biologist

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OBSERVATIONS ON THE SPAWNING OF PHILIPPINE TUNA

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The study of the life histories of the several commercially important species of tuna in the Pacific Ocean has been greatly accelerated by the postwar expansion of the tuna fishery in that area. One phase of their life histories that has aroused considerable interest and speculation, both scientific and popular, concerns the time and place of spawning. Some research has been done on this in the Mediterranean area, and although incomplete, much has been learned of the early life history of the tuna of that region. In the Pacific, on the other hand, almost nothing was known of their spawning habits until Schaefer and Marr (1948) and Marr (1948) published a series of short papers on the spawning and juvenile forms of the genera *Neothunnus*, *Katsuwonus*, *Euthynnus*, and *Auxis*. They demonstrated, by the collection of juveniles, that these four genera spawn along the west coast of Central America and that the genus *Katsuwonus* also spawns in the northern Marshall Islands.

In the pelagic fish studies of the Philippine Fishery Program [1] of the Fish and Wildlife Service information on all phases of the biology of the Philippine tuna has been sought since October 1947. One part of this operation has been concerned with the accumulation of data on the degree of maturity of the fish caught and the search for juvenile forms. The data were collected on the oceanographic research vessel, *Spencer F. Baird*, from fish caught principally by trolling during the period October 1947 through November 1948.

CLASSIFICATION OF GONADS

Determinations of the degree of maturity were made as the fish were captured, in accordance with the criteria described by Marr (1948). To the stages of gonad development as classified by him, immature, ripening, ripe, spawning, and spent, was added the term "unknown" for those fish in which the gonads were insufficiently developed to determine the sex, or the degree of maturity was not noted for some reason.

Marr (1948) suggested that after the fish spawn for the first time the gonads do not reduce to the small size prevailing before first maturity. The size of the gonads during the so-called "resting stage" between spawning periods is not known. It is impossible at the present time to distinguish externally between gonads ripening for the first time and those that are reduced in size after spawning. At some time during the spawning cycle the two stages could presumably appear identical. There seems to be no doubt that a certain percentage of fish designated as ripening in the present study were in this resting stage.

Although this classification gives a good estimate of the gross changes that occur during the maturation of the gonads, it is not sufficiently precise to evaluate properly the gonad condition in a more comprehensive study. It has been the experience of biologists of the Philippine Fishery Program that the external appearance of the gonads is often deceiving and considerable experience is required to classify these organs correctly.

Many factors contribute to the variations in the external appearance of the gonads that might influence the judgment of the observer. Among these are the size of the specimen, the number of times it had spawned, variations in size and appearance of gonads of seemingly identical specimens, the physical condition of the fish, and there are, no doubt, other factors. The development of a method of ac-

[1] A part of the Philippine Rehabilitation Program authorized by the Philippine Rehabilitation Act of 1946, title 50, App. U. S. Code, Sec. 1789.

curately evaluating the gonad condition will require considerable research. It appears that the ovary, rather than the testes, offers the more satisfactory means of establishing an index to maturity. It may be that after considerable study of the maturation of the eggs in the ovary, a reference point can be located from which small identical samples may be taken. The diameters of the eggs in the sample could then be tabulated and it may be found that combinations of certain percentages of various size classes will provide a formula for determining more accurately the various degrees of maturity.

EUTHYNNUS YAITO (KISHINOUYE)

The field data for this species are presented in tables 1, 2, and 3 and figure 1.

Immature fish were captured only from March through July. The immature females averaged larger than the males, which may have been the result of an inadequate sample. Again, it may indicate that the females grow more rapidly or reach maturity at a greater age and a larger size, than the males, if the growth rate of the two sexes is equal. In addition to the immature fish of which the sex could be determined, specimens were taken of which the sex could not be identified by field methods. The gonads of these fish were elongate, thread-like bodies barely visible in the enveloping membrane and in all cases the weight of the gonads and attached membranes was less than 1 gram.

Ripening fish of both sexes and in all stages of ripening were captured throughout the year. This suggests that spawning is not confined to any particular period. Also, based on the size range of ripening and ripe specimens in the collections, it is evident that *E. yaito* begins to ripen at a smaller size than this sample of ripening fish would indicate.

The difficulty of distinguishing ripe from spent males has, undoubtedly, introduced some degree of error in the number of ripe males reported. The tendency has been to classify males as ripe rather than spent. On the other hand, no error of this nature should occur with the females. Considerable range in the size of ripe gonads was noted not only throughout the size range, but among individuals of similar size.

Spawning and spent fish were taken throughout the period of operation. No running-ripe females were seen although specimens were secured in which the eggs were lying free in the posterior part of the ovary. Spawning males were common, however, often extruding milt on the deck when brought aboard ship.

There is only one specific reference to the spawning of *E. yaito* in the literature. Kishinouye (1923) stated that spawning takes place in Taiwan (Formosa) about May. This observation was based on a single 115 mm. specimen collected from that area during the latter part of August. Schaefer and Marr (1948) collected a running-ripe female of

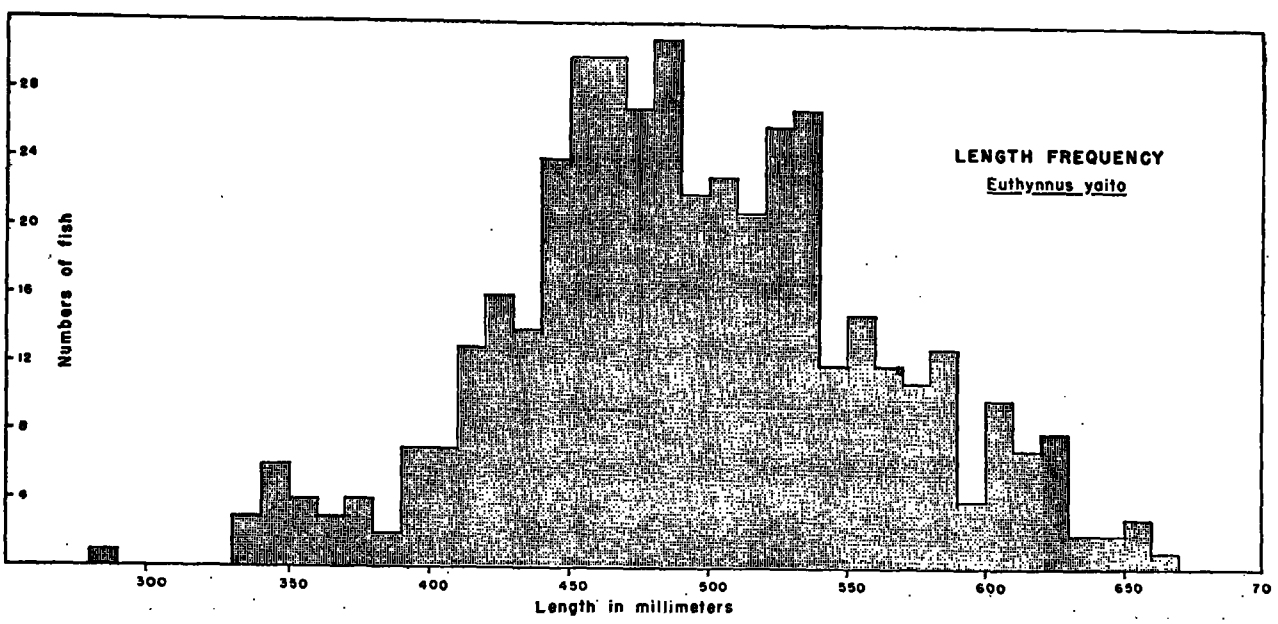

FIGURE 1.—Length-frequency distribution of *Euthynnus yaito* taken in Philippine waters from October 1947 through November 1948.

a closely related species, *Euthynnus lineatus*, off the west coast of Central America in April.

The presence of fish in all stages of sexual development during the entire year in Philippine waters seems indicative of year-round spawning in that area. Although its is certain that spawning does occur throughout the year, the sample is not sufficiently large to determine possible seasonal variations in intensity during that time.

KATSUWONUS PELAMIS (LINNAEUS)

The data for *Katsuwonus pelamis* are presented in tables 4, 5, and 6 and figure 2.

Only an occasional immature fish was taken during the entire period of operations. The poor representation of small, immature fish of all species in the collections can be explained partly by the fact that the trolling gear was designed primarily for larger fish and, consequently, smaller specimens could not readily take the lure.

TABLE 1.—*Monthly summary of all specimens of* Euthynnus yaito *taken by the* Spencer F. Baird, *October 1947–November 1948*

Month	Immature	Ripening	Ripe	Spawning	Spent	Unknown	Total
ALL FISH							
October							
November			1				1
December		7	2	15		2	26
January		1	10	27	1		39
February		26	23	9	37	14	109
March			5	6	1	2	14
April	5		6	10	17	1	39
May	10	14	11	34	16	4	89
June	2	1	14	2	4		23

TABLE 1.—*Monthly summary of all specimens of* Euthynnus yaito *taken by the* Spencer F. Baird, *October 1947–November 1948*—Con.

Month	Immature	Ripening	Ripe	Spawning	Spent	Unknown	Total
ALL FISH—Continued							
July	2	1	5	6	4		18
August			1				1
September							
October		1	1	5	7		14
November		46	9	23	8	1	87
Total	19	97	88	137	95	24	460
MALES							
October							
November							
December		3	1	15			19
January		1	4	16			21
February		25	23	6		1	55
March			1	3			4
April	3		3	9			15
May		4	8	32		1	45
June		1	9	2			12
July	2		1	6			9
August			1				1
September							
October				5	4		9
November		18	5	23	3		49
Total	5	52	56	117	7	2	239
FEMALES							
October							
November			1				1
December		4	1			2	7
January			6	13	1		20
February		1		3	37	1	42
March			4	3	1	1	9
April	5		3	1	17		26
May	7	10	3	2	16		38
June	2		5		4		11
July		1	4		4		9
August							
September							
October		1	1		3		5
November		28	4		5		37
Total	14	45	32	22	88	4	205

TABLE 2.—*Length-frequency and degree of maturity of troll-caught* Euthynnus yaito *from Philippine waters, taken by the* Spencer F. Baird, *October 1947–November 1948*

Length in millimeters	Immature			Ripening			Ripe			Spawning			Spent			Unknown [1]		
	All	Male	Female	All	Male	Female	All	Male	Female	All	Male	Female	All	Male	Female	All	Male	Female
280–289																1		
290–299																		
300–309																		
310–319																		
320–329																		
330–339	2		2													1		
340–349	4	1	3				1	1								2		
350–359	2	1	1													3		
360–369				2		2										1		
370–379	1		1	2	1	1				1	1							
380–389	3	3		2	1	1												
390–399	1		1	1		1												
400–409	1		1	2		2	1		1	2	2		1		1			
410–419	1		1	4		4	1		1							1		
420–429	1		1	5	2	3	4	3	1	1	1					2		
430–439				1	1		4	2	2	1	1		1		1			
440–449	1		1	1		1	4	3	2	3	3		4		4	2		
450–459	1		1	1		1	6	1	5	5	4	1	4		4	1		
460–469	1		1	12	6	6	1		1	2	2		6		6			
470–479				11	8	3	2	2		12	10	2	2		2	2		1
480–489				11	4	7	3	2	1	9	8	1	8		8			
490–499				10	7	3	6	4	2	8	7	1	1		1	2	2	

See footnote at end of table.

TABLE 2.—*Length-frequency and degree of maturity of troll-caught* Euthynnus yaito *from Philippine waters, taken by the* Spencer F. Baird, *October 1947–November 1948*—Continued

Length in millimeters	Immature			Ripening			Ripe			Spawning			Spent			Unknown [1]		
	All	Male	Female	All	Male	Female	All	Male	Female	All	Male	Female	All	Male	Female	All	Male	Female
500–509				5	3	2	10	7	3	6	5	1	11		11			
510–519				4	3	1	5	4	1	6	6		7	2	5	1		1
520–529				3	1	2	3	3		8	5	3	9	1	8			
530–539				3	1	2	4	4		4	3	1	9		9	1	1	
540–549				5	4	1	2	1	1	13	11	2	6		6			
550–559				4	3	1	7	4	3	5	5		10	2	8			
560–569				2	2		4	2	2	5	4	1	5	2	3	1	1	
570–579				2	1	1	5	3	2	5	4	1	2		2	1		
580–589							4	2	2	6	6		3		3	1		
590–599				2	2		1		1	6	5	1	2		2			
600–609							3	1	2	6	3	3	2		2			
610–619										5	5							
620–629							1	1		5	3	2	1		1			
630–639				1	1		2	2		3	2	1	1		1	1		
640–649							1	1		6	5	1						
650–659							1	1		1	1							
660–669							1	1		1	1							
670–679				1	1					2	2							
680–689							1	1										
Total	19	5	14	97	52	45	88	56	32	137	115	22	95	7	88	24	4	2

[1] Includes those specimens in which the sex and gonad condition were not known or one or other was unknown.

TABLE 3.—*Locality, length, sex, degree of maturity, and gonad weight of* Euthynnus yaito *taken by the* Spencer F. Baird *in Philippine waters, October 1947–November 1948*

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1947					
Nov. 11	Zamboanga	580	Female	Ripe	135.0
Dec. 5	Sulu Archipelago	585	do	do	141.0
Dec. 14	Pilas Island, Sulu Archipelago	621	do	Ripening	123.5
14	do	557	do	do	111.3
14	do	625	Male	Spawning	103.5
14	do	582	do	Ripe	37.0
14	do	533	do	Ripening	73.1
14	do	529	do	do	52.8
14	do	557	do	do	91.2
14	do	596	do	Spawning	84.4
Dec. 15	Zamboanga	584	do	do	130.0
15	do	607	do	do	140.0
15	do	570	do	do	120.0
15	do	535	do	do	98.0
15	do	566	Female		99.5
15	do	545	Male	Spawning	162.5
15	do	491	do	do	73.0
15	do	499	Female		69.0
15	do	471	Male	Spawning	49.0
15	do	488	Female	Ripening	47.0
15	do	470	Male	Spawning	43.0
15	do	479	do	do	74.0
15	do	474	do	do	46.5
15	do	455	do	do	39.0
15	do	466	do	do	63.0
Dec. 16	do	592	do	do	86.0
16	do	462	Female	Ripening	39.0
1948					
Jan. 7	South Sulu Sea	594	Male	Spawning	133.6
7	do	603	Female	do	82.4
7	do	556	Male	do	53.2
7	do	618	do	do	129.0
7	do	578	do	do	72.4
7	do	593	Female	do	162.5
7	do	613	Male	do	81.0
7	do	545	do	do	70.0
7	do	620	do	do	102.5
7	do	637	do	Ripening	97.5
7	do	656	do	Spawning	178.5
7	do	566	Female	Spent	62.3
7	do	601	do	Ripe	154.5
Jan. 12	do	512	do	do	70.0

[1] Preserved in the round.

TABLE 3.—*Locality, length, sex, degree of maturity, and gonad weight of* Euthynnus yaito *taken by the* Spencer F. Baird *in Philippine waters, October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
Jan. 14	Pilas Island, Sulu Archipelago.	600	Female	Spawning	140.0
14	do	526	Male	do	104.0
14	do	611	do	do	113.5
14	do	605	Female	do	177.5
14	do	481	do	do	63.0
14	do	550	Male	Ripe	101.0
14	do	477	Female	Spawning	67.7
14	do	634	Male	Ripe	133.7
14	do	545	do	Spawning	98.7
14	do	571	Female	do	136.0
14	do	540	do	do	74.6
14	do	620	do	do	133.5
14	do	591	Male	do	92.7
14	do	601	Female	do	126.0
14	do	497	Male	do	53.3
14	do	430	Female	Ripe	41.0
14	do	562	do	do	59.5
14	do	457	do	do	58.5
14	do	454	Male	Spawning	79.1
14	do	484	do	do	61.6
14	do	496	do	do	55.0
14	do	485	Female	Ripe	72.0
14	do	523	Male	do	64.0
14	do	542	do	do	75.0
14	do	522	Female	Spawning	75.0
14	do	540	do	do	113.5
14	do	560	do	do	98.0
Feb. 19	Port Santa Maria, Zamboanga Peninsula.	550	Male	Ripe	37.5
19	do	480	Female	Spent	19.4
19	do	622	Male	Ripe	188.6
19	do	530	Female		37.7
19	do	645	(1)		
19	do	576	(1)		
19	do	476	(1)		
19	do	424	(1)		
19	do	422	(1)		
19	do	582	(1)		
19	do	446	(1)		
19	do	443	(1)		
19	do	687	Male	Ripe	150.0
19	do	565	do	Spawning	43.0

TABLE 3.—*Locality, length, sex, degree of maturity, and gonad weight of* Euthynnus yaito *taken by the* Spencer F. Baird *in Philippine waters, October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
Feb. 19	Port Santa Maria, Zamboanga Peninsula.	558	Female	Spent	37.6
19	do	560	do	do	37.5
19	do	510	Male	Spawning	34.5
19	do	503	do	Ripening	165.0
19	do	535	Female	Spent	63.1
19	do	540	Male	Ripening	27.5
19	do	510	Female	Spent	33.8
19	do	562	Male	Ripening	33.0
19	do	642	do	Ripe	110.3
19	do	556	do	do	58.1
19	do	592	do	Ripening	44.2
19	do	651	do	Ripe	90.5
19	do	575	Female	Spent	54.4
19	do	600	do	do	69.1
19	do	558	Male	Spawning	67.0
19	do	564	do	Ripening	26.0
19	do	673	do	do	221.6
19	do	555	do	Spawning	8.3
19	do	520	Female	Spent	48.3
19	do	510	do	do	44.9
19	do	560	Male	Ripe	69.7
19	do	508	Female	Spent	29.8
19	do	570	Male	Ripening	28.2
19	do	560	do	do	21.9
19	do	462	do	do	15.6
19	do	540	do	do	33.7
19	do	587	Female	Spent	42.6
19	do	494	Male	Ripening	28.2
19	do	509	Female	Spent	48.8
19	do	490	do	do	18.6
19	do	472	Male	Ripe	25.2
19	do	516	Female	Spent	25.3
19	do	466	do	Ripening	14.7
19	do	562	do	Spent	35.2
19	do	596	do	do	51.5
19	do	668	Male	Ripe	125.5
19	do	558	Female	Spent	41.4
19	do	530	do	do	48.3
19	do	530	do	do	34.7
19	do	532	Male	Ripe	26.1
19	do	595	do	Ripening	22.1
19	do	520	do	Ripe	32.3
19	do	550	do	do	43.5
19	do	515	do	do	27.8
19	do	509	do	do	34.3
19	do	603	Female	Spent	51.7
19	do	515	do	do	28.5
19	do	501	Male	Ripening	18.5
19	do	471	Female	Spawning	14.5
19	do	573	Male	Ripe	95.9
19	do	554	do	Ripening	51.7
19	do	559	do	do	51.6
19	do	460	do	do	7.6
19	do	484	Female	Spent	24.8
19	do	500	do	do	29.3
19	do	463	Male	Ripening	10.4
19	do	470	Female	Spent	17.9
19	do	466	do	do	11.4
19	do	475	Male	Ripening	8.3
19	do	548	do	do	36.8
19	do	533	Female	Spent	23.4
19	do	518	Male	Ripening	13.4
19	do	526	Female	Spent	26.8
19	do	510	Male	Ripening	18.5
19	do	498	do	Ripe	21.2
19	do	534	Female	Spawning	44.9
19	do	472	Male	Ripening	7.6
19	do	514	do	do	13.1
19	do	523	Female	Spent	28.4
19	do	467	do	do	16.7
19	do	477	Male		12.5
19	do	493	do	Ripe	29.3
19	do	502	do	do	22.7
19	do	522	Female	Spent	38.5
19	do	507	Male	Ripe	17.9
19	do	483	do	do	9.9
19	do	477	do	do	11.1
19	do	501	Female	Spent	21.7
19	do	503	Male	Ripe	15.9
19	do	480	Female	Spent	17.3
19	do	485	Male	Ripe	22.1
19	do	460	do	Ripening	6.5
19	do	510	do	Spawning	74.1
19	do	527	Female	Spent	28.3

[2] Gonads insufficiently developed to determine the sex.

TABLE 3.—*Locality, length, sex, degree of maturity, and gonad weight of* Euthynnus yaito *taken by the* Spencer F. Baird *in Philippine waters, October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
Feb. 19	Port Santa Maria, Zamboanga Peninsula.	494	Female	Spawning	44.6
19	do	458	do	Spent	13.6
19	do	478	Male	Ripening	19.2
19	do	519	Female	Spent	32.2
19	do	488	do	do	23.1
19	do	508	do	do	23.5
Feb. 21	Zamboanga	638	Male	Spawning	223.5
Feb. 23	Margosatubig, Moro Gulf	339	(2)	Immature	
23	do	355	(2)	do	
23	do	345	(2)	do	
23	do	355	(2)	do	
Mar. 2	Bangka Passage, Celebes	283	(2)	do	1
2	do	283	(?)	Ripe	28.1
2	do	571	Female	do	161.2
2	do	521	do	Spawning	80.9
2	do	542	do	Spent	56.3
2	do	520	Male	Spawning	56.9
2	do	498	Female		48.9
2	do	500	do	Spawning	69.3
Mar. 13	West coast of Panay	575	Male	do	159.2
13	do	553	Female	Ripe	185.7
13	do	508	do	do	220.0
13	do	505	do	do	119.0
13	do	406	Male	Spawning	38.7
13	do	455	Female	do	43.8
Apr. 6	North Sulu Sea	447	Male	do	39.8
6	do	440	Female	Spent	24.0
6	do	473	Male	Spawning	61.7
6	do	406	Female	Spent	16.0
6	do	443	do	do	21.7
6	do	443	do	do	51.5
6	do	448	Male	Ripe	36.8
6	do	426	Female	Immature	6.8
Apr. 8	Sulu Archipelago	600	Male	Ripe	56.9
8	do	543	Female	Spent	50.4
8	do	485	do	do	24.9
8	do	450	do	Immature	8.9
8	do	412	do	do	3.4
8	do	395	do	do	1.4
8	do	632	do	Spawning	66.4
8	do	530	do	Spent	42.4
8	do	472	do	do	24.4
8	do	490	Male	Ripe	66.3
8	do	540	Female	Spent	66.2
8	do	509	do	do	30.4
8	do	663	Male	Spawning	99.9
8	do	500	Female	Spent	31.1
8	do	553	Male	Spawning	70.3
8	do	542	Female	Spent	46.5
8	do	525	Male	Spawning	38.1
8	do	419	(?)	Immature	4.6
8	do	561	Female	Spent	38.2
8	do	592	do	Ripe	116.1
8	do	648	Male	Spawning	123.6
8	do	545	Female	Spent	
8	do	585	do	do	66.0
8	do	375	do	Immature	1.3
Apr. 17	do	484	do	Spent	33.8
17	do	484	Male	Spawning	10.5
17	do	504	Female	Ripe	44.9
17	do	593	do	Spent	94.0
Apr. 18	do	567	Male	Spawning	46.1
18	do	485	do	do	29.0
Apr. 21	West Zamboanga Peninsula.	543	Female	Ripe	83.6
May 5	North Sulu Sea	511	Male	Spawning	12.0
5	do	532	Female	Ripening	18.2
5	do	495	Male	Spawning	10.8
5	do	452	Female	Ripening	10.2
5	do	475	Male	do	6.5
5	do	499	do	do	6.5
5	do	498	Female	do	20.1
5	do	494	do	do	17.0
May 7	Pilas Island, Sulu Archipelago.	574	Male	Ripe	23.8
7	do	515	Female	Spawning	41.5
7	do	556	do	Ripe	92.0
7	do	359	(?)	Immature	
7	do	548	Male	Spawning	85.1
7	do	527	do	do	25.0
7	do	505	Female	Spent	14.7
7	do	514	Male	Spawning	22.1

TABLE 3.—*Locality, length, sex, degree of maturity, and gonad weight of* Euthynnus yaito *taken by the* Spencer F. Baird *in Philippine waters, October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
May 7	Pilas Island, Sulu Archipelago.	547	Male	Spawning	39.1
7	do	608	do	do	100.6
7	do	570	do	Ripe	71.8
7	do	591	do	Spawning	41.4
7	do	540	do	do	44.5
7	do	500	Female	Spent	27.5
7	do	511	do	Ripening	20.8
7	do	400	do	Immature	3.1
7	do	521	do	Ripening	22.5
7	do	539	Male	Ripe	29.3
7	do	548	do	Spawning	53.5
May 8	do	547	Female	Ripening	42.0
8	do	454	Male	Spawning	3.4
8	do	501	Female	Ripening	44.8
8	do	549	Male	Spawning	54.5
8	do	644	Female	do	96.5
8	do	539	Male	do	25.9
8	do	500	do	do	32.5
8	do	527	Female	Spent	35.7
8	do	530	do	do	41.0
8	do	525	do	do	39.0
8	do	536	do	do	36.9
8	do	532	do	do	34.5
8	do	531	do	do	26.2
8	do	521	Male	Spawning	21.9
8	do	620	Female	Spent	86.5
8	do	498	Male	Ripening	11.5
8	do	492	do	Spawning	22.0
8	do	498	Female	Ripening	18.2
8	do	361	(?)	Immature	--------
8	do	345	(?)	do	--------
8	do	459	Male	Spawning	15.5
8	do	566	do	do	42.6
8	do	554	do	do	21.9
8	do	578	Female	Ripening	15.5
8	do	513	Male	Immature	3.3
May 10	Moro Gulf, Mindanao	515	do	Ripe	58.1
10	do	531	do	do	59.8
May 12	do	476	do	Ripening	7.3
12	do	383	do	Immature	2.0
12	do	343	Female	do	4.2
12	do	344	Male	do	2.5
May 15	Davao Gulf, Mindanao.	348	Female	do	3.8
15	do	343	do	do	2.2
15	do	356	do	do	7.2
15	do	358	Male	do	2.1
15	do	331	Female	do	4.8
15	do	334	do	do	3.4
15	do	435	do	Spent	13.1
May 17	Sulu Archipelago	564	do	Ripe	51.5
17	do	648	Male	Spawning	84.5
17	do	677	do	do	65.8
17	do	626	Female	Spent	58.9
17	do	636	Male	Ripe	35.0
17	do	637	Female	Spent	51.5
17	do	605	Male	Spawning	71.0
17	do	641	do	do	69.5
17	do	566	do	do	106.0
17	do	642	do	do	97.5
17	do	612	do	do	65.5
17	do	549	do	do	54.0
17	do	587	do	do	52.0
17	do	583	do	do	732.0
17	do	516	do	do	45.0
17	do	532	do	Ripe	19.9
17	do	499	do	Spawning	31.0
17	do	634	do	do	35.5
17	do	604	Female	Ripe	143.4
17	do	554	do	Spent	27.8
May 18	do	556	do	do	51.0
18	do	568	Male	Ripe	46.2
18	do	542	Female	Spent	37.5
18	do	557	do	do	35.5
June 16	North Sulu Sea	485	do	do	12.7
16	do	463	do	do	15.0
16	do	461	do	Immature	3.2
16	do	442	do	do	1.2
16	do	515	Male	Spawning	10.6
16	do	467	Female	Spent	15.6
16	do	479	Male	Spawning	15.8
16	do	458	Female	Spent	13.6
June 27	do	512	Male	Ripe	37.5
27	do	580	do	do	85.5
27	do	508	do	do	35.8
27	do	498	do	do	35.2

TABLE 3.—*Locality, length, sex, degree of maturity, and gonad weight of* Euthynnus yaito *taken by the* Spencer F. Baird *in Philippine waters, October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
June 29	Busuanga Islands, China Sea.	448	Male	Ripe	21.0
29	do	431	Female	do	14.0
29	do	436	Male	do	9.7
29	do	425	do	do	6.2
29	do	491	Female	do	70.0
29	do	428	Male	do	21.0
29	do	492	Female	do	42.4
29	do	401	do	do	24.5
29	do	362	Male	Ripening	2.0
29	do	454	Female	Ripe	18.0
29	do	450	Male	do	18.3
July 11	South Sulu Sea	388	do	Immature	2.0
11	do	486	do	Spawning	27.3
July 12	Southwest Sulu Sea	385	do	Immature	2.0
12	do	484	do	Spawning	37.0
July 14	Balabac Island, Sulu Sea.	582	Female	Spent	89.7
14	do	555	do	do	104.7
14	do	548	Male	Spawning	75.5
14	do	549	do	do	82.5
14	do	550	Female	Spent	92.5
14	do	450	do	Ripe	45.0
14	do	406	do	Ripening	8.0
14	do	565	do	Ripe	87.0
14	do	611	Male	Spawning	178.0
14	do	546	do	do	48.5
14	do	571	Female	Spent	25.9
14	do	508	Male	Ripe	41.3
14	do	458	Female	do	63.5
14	do	457	do	do	50.0
Aug. 9	Sibuguey Bay, Moro Gulf.	348	Male	do	18.0
Oct. 31	North Palawan, China Sea.	467	do	Spawning	9.0
31	do	432	do	do	11.0
31	do	524	Female	Spent	25.0
31	do	425	Male	Spawning	9.0
31	do	412	Female	Ripening	9.0
31	do	507	Male	Spent	15.0
31	do	448	Female	do	12.0
31	do	473	Male	Spawning	8.0
31	do	455	Female	Spent	25.0
31	do	550	Male	do	10.0
31	do	503	do	Spawning	10.0
31	do	550	do	Spent	14.0
31	do	463	Female	Ripe	50.0
31	do	511	Male	Spent	5.0
Nov. 2	do	496	do	Ripening	5.0
Nov. 4	do	550	do	Spent	6.0
4	do	565	do	do	10.0
4	do	465	Female	do	20.0
4	do	464	do	do	26.0
4	do	450	do	do	10.0
Nov. 5	Northeast Palawan	428	Male	Ripe	8.0
Nov. 6	North Palawan	485	do	Ripening	3.0
6	do	481	Female	do	6.0
6	do	490	Male	do	3.0
6	do	482	do	do	6.0
6	do	487	Female	do	18.0
Nov. 7	Northeast Palawan	478	do	do	13.0
7	do	482	do	do	14.0
7	do	473	Male	do	7.0
7	do	481	Female	do	16.0
7	do	470	Male	do	7.0
7	do	495	do	do	7.0
7	do	475	do	do	4.0
7	do	402	Female	do	8.0
7	do	380	Male	do	4.0
7	do	420	do	do	4.0
Nov. 8	West Sulu Sea	420	Female	do	9.0
8	do	420	do	do	9.0
8	do	430	Male	do	2.0
8	do	414	Female	do	8.0
8	do	410	(?)	Immature	--------
Nov. 9	Southwest Sulu Sea	416	Female	Ripening	6.0
9	do	428	do	do	10.0
9	do	477	Male	Spawning	16.0
9	do	521	do	do	12.0
9	do	522	Female	Ripening	24.0
9	do	508	do	Ripe	22.0
9	do	441	Male	Spawning	10.0
Nov. 10	do	520	do	Ripe	10.0
10	do	468	Female	Ripening	16.0
Nov. 11	do	442	do	do	8.0
11	do	475	do	do	6.0
11	do	535	do	do	20.0

TABLE 3.—*Locality, length, sex, degree of maturity, and gonad weight of* Euthynnus yaito *taken by the* Spencer F. Baird *in Philippine waters, October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
Nov. 11	Southwest Sulu Sea	508	Female	Ripening	18.0
11	do	518	Male	Ripe	6.0
11	do	480	do	Ripening	4.0
11	do	465	do	do	4.0
11	do	506	do	do	8.0
11	do	462	Female	do	14.0
11	do	480	Male	Spawning	12.0
11	do	503	do	do	8.0
11	do	472	Female	Ripening	14.0
11	do	485	do	do	12.0
Nov. 12	do	490	Male	do	4.0
12	do	430	do	Ripe	6.0
12	do	575	do	Spawning	48.0
12	do	585	do	do	50.0
12	do	585	do	do	48.0
12	do	545	Female	Spent	44.0
Nov. 13	West Sulu Sea	385	do	Ripening	10.0
13	do	391	do	do	10.0
13	do	500	Male	Spawning	22.0
13	do	505	do	do	17.0
13	do	490	do	do	23.0
13	do	525	do	Spent	9.0
13	do	482	Female	do	19.0
13	do	485	Male	Spawning	12.0
13	do	487	do	do	12.0
13	do	470	do	do	17.0
13	do	475	do	do	18.0
13	do	472	do	do	12.0
Nov. 16	South Sulu Sea	420	do	Ripening	5.0
16	do	460	do	do	12.0
16	do	410	Female	do	8.0
16	do	460	do	do	14.0
16	do	480	Male	do	11.0
Nov. 17	do	445	Female	Ripe	40.0
17	do	440	Male	do	30.0
17	do	410	Female	do	30.0
17	do	670	Male	Spawning	145.0
17	do	649	do	do	78.0
17	do	625	do	do	90.0
17	do	428	Female	Ripe	40.0
17	do	467	do	Ripening	10.0
Nov. 22	North Sulu Sea	405	Male	Spawning	20.0
22	do	375	Female	Ripening	4.0
22	do	442	Male	Spawning	20.0
22	do	400	do	do	10.0
Nov. 23	West of Mindoro	365	Female	Ripening	6.0
23	do	360	do	do	8.0
23	do	370	Male	Spawning	8.0

Although the sample of ripening fish is too small to permit definite conclusions, there are indications of the possible trend in the maturation of this species. Those fish caught during the first half of the year appear to have ripening gonads more fully developed than those taken during the latter half. This suggests that spawning occurs mainly during the late spring and summer months. Ripe *K. pelamis* were taken throughout the islands during the entire year, but in the greatest abundance in April, May, June, and July. The larger number of ripe fish taken during this period is probably indicative of a period of more intensive spawning.

Spawning and spent fish were taken from March through July and scattered specimens during the remainder of the year. The majority of spawning *K. pelamis* were males, but the larger percentage of spent fish were females. From the information available the reversal of sex dominance in spawning and spent fish cannot be explained. The lack of spent males may be partly explained as resulting from misidentification of the stage of maturity. At the present time there is no way to determine accurately the differences between males approaching spawning and those past the peak of spawning. The larger percentage of spawning males caught probably can be explained in that the aggressiveness of the male during spawning makes him more prone to strike at a lure.

The only reference available on the spawning of this species in the western Pacific (Kishinouye 1923) indicates that in Japan *K. pelamis* spawns from May to August. This period coincides with what is believed to be the peak of spawning in Philippine waters. Schaefer and Marr (1948) are of the opinion that along the west coast of Central America *pelamis* spawns at least from January into March. Although there is evidence that it also spawns during this time in Philippine waters, spawning of the greatest intensity occurs during the early summer months.

The data show that in Philippine waters *Katsuwonus pelamis* spawns through the year. The principal spawning period, however, begins in February and reaches its peak in June. Spawning activity then decreases until a period of minimum activity is reached during September and October followed by a slight increase in November and December and another decline during January. A few ripe fish taken during September and December suggests that some spawning may also occur in October and January, although no spawning or spent fish were caught during those months.

NEOTHUNNUS MACROPTERUS (TEMMINCK AND SCHLEGEL)

In tables 7, 8, and 9 and figure 3 are presented the field data for *Neothunnus macropterus* (yellowfin tuna).

Almost one-half (48.5 percent) of the yellowfin tuna caught were immature and too poorly developed to yield information on spawning. The sex of 61 percent of the immature fish could not be determined by the usual field methods.

870654°—50——2

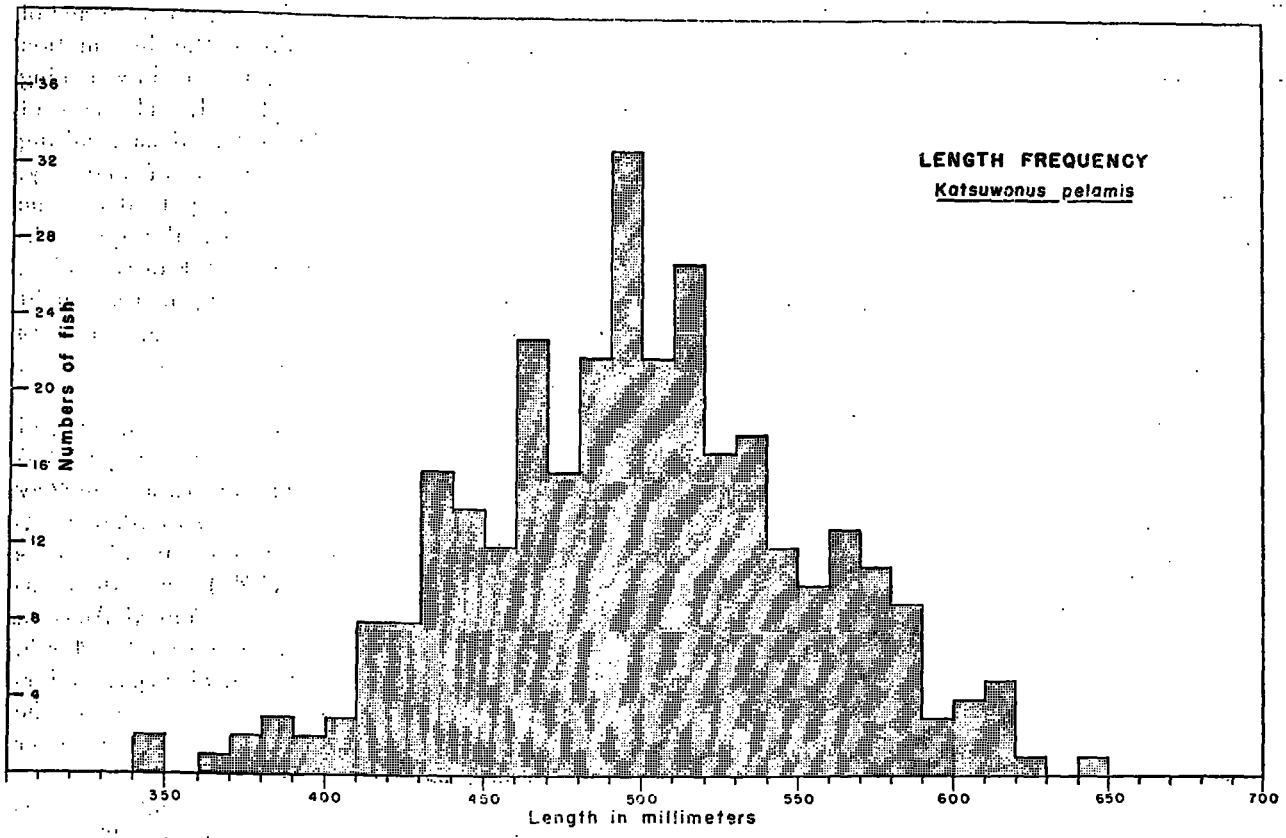

FIGURE 2.—Length-frequency distribution of *Katsuwonus pelamis* taken in Philippine waters from October 1947 through November 1948.

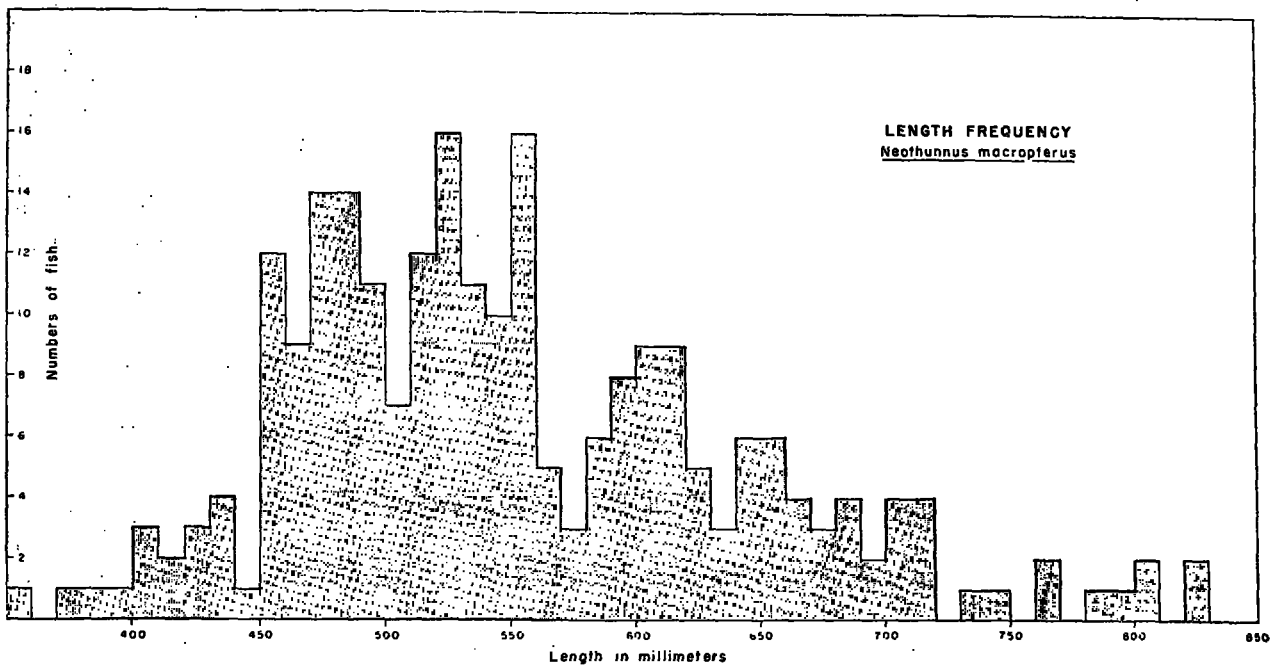

FIGURE 3.—Length-frequency distribution of *Neothunnus macropterus* taken in Philippine waters from October 1947 through November 1948.

TABLE 4.—*Monthly summary of all specimens of troll-caught* Katsuwonus pelamis, *taken by the* Spencer F. Baird, *October 1947–November 1948*

Month	Immature	Ripening	Ripe	Spawning	Spent	Unknown	Total
ALL FISH							
October							
November							
December			6	9		10	25
January		1					1
February		5	2	2		1	10
March		5	7	7	1		20
April	5	1	31	7	1	2	47
May	1	6	33	8	11	1	60
June		6	42	8	33		89
July			25	13	1		39
August		4	11	2	1		18
September			3		1		4
October							
November		2	13	4	1	2	22
Total	6	30	173	60	50	16	335
MALES							
October							
November							
December			3			5	8
January							
February		2	1				3
March		6		2	1		9
April	1		18	1	1		21
May		3	8	5	11		27
June		2	20		27		49

TABLE 4.—*Monthly summary of all specimens of troll-caught* Katsuwonus pelamis, *taken by the* Spencer F. Baird, *October 1947–November 1948*—Continued

Month	Immature	Ripening	Ripe	Spawning	Spent	Unknown	Total
MALES—Continued							
July			13		1		14
August		4	4		1		9
September			3		1		4
October							
November			8		1		9
Total	1	17	78	8	44	5	153
FEMALES							
October							
November							
December			3	9		5	17
January		1					1
February		3	1	2			6
March			7	5			12
April	4	1	13	6		2	26
May	1	3	25	3			32
June		4	22	8	6		40
July			12	13			25
August			7	2			9
September							
October							
November		1	5	4			10
Total	5	13	95	52	6	7	178

TABLE 5.—*Comparison of the length-frequencies of* Katsuwonus pelamis *at several stages of gonad development, taken in Philippine and Marshall Islands waters* [1]

Length in millimeters	Immature				Ripening				Ripe				Spawning				Spent			
	Philippines Male	Marshall Islands Male	Philippines Female	Marshall Islands Female	Philippines Male	Marshall Islands Male	Philippines Female	Marshall Islands Female	Philippines Male	Marshall Islands Male	Philippines Female	Marshall Islands Female	Philippines Male	Marshall Islands Male	Philippines Female	Marshall Islands Female	Philippines Male	Marshall Islands Male	Philippines Female	Marshall Islands Female
340–349											1		1							
350–359																				
360–369	1																			
370–379	1		1																	
380–389	2				1															
390–399	1						1			1										
400–409							1				1								1	1
410–419									6										1	
420–429					1		2		2		1		1						1	
430–439					1	1	6		5	4	2	1	2						1	1
440–449				2	2		1		5	6	4	1	3						2	1
450–459		1		1		4			3	9	3	4	3	1	1				1	1
460–469		1				6	1	1	7	5	8	4	2	1		1		1	2	
470–479						1	1		6	5	2	3	6	1					1	1
480–489						1	1		7	4	7	3	1		1		2		1	1
490–499					1		1		9	3	6	2	6		2		1		2	
500–509					1				7	3	8		3		1				3	
510–519					2				10		7	2	4		2				5	
520–529					1				3		5		5						3	
530–539									4	1	5	1	6						5	
540–549									3	5	4	3	1				1		2	
550–559							2		3	2	1	1	2						3	
560–569					1				7	2	1	1	2						3	
570–579					1				3	4	3	1	2				1		1	
580–589									2	1	5				1				3	
590–599					1					1	1	1							1	
600–609									1	1	2									
610–619										2		1	1				1		2	1
620–629									1	3	1	3								
630–639									1	2		1								
640–649										3		2	1							
650–659										4		6								
660–669		1								6		2								
670–679										3										1
680–689										9										1
690–699										6		1								
700–709										1		1								
710–719										1										
720–729																				
Total	5	3	1	3	13	13	17	1	95	97	78	45	52	3	8	1	6	1	44	9

[1] Length-frequency data on Marshall Islands specimens taken from Marr (1948).

TABLE 6.—*Locality, length, sex, degree of maturity, and gonad weight of* Katsuwonus pelamis *taken in Philippine waters by the* Spencer F. Baird, *October 1947–November 1948*

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1947					
Dec. 11	Sulu Archipelago	540	Male	Unknown	86.0
11	do	505	Female	Ripe	168.2
11	do	485	do	Unknown	90.5
11	do	500	do	Ripe	119.9
11	do	502	Male	Uknown	68.5
11	do	495	do	Spawning	77.2
11	do	512	do	do	51.2
11	do	491	Female	Ripe	126.1
11	do	475	Male	Spawning	59.3
11	do	490	do	do	40.5
11	do	500	do	do	74.5
11	do	490	do	do	71.0
Dec. 12	do	479	do	do	64.7
12	do	497	Female	Unknown	90.0
12	do	510	Male	Ripe	72.0
12	do	532	do	Spawning	74.0
Dec. 13	do	498	do	Unknown	32.0
13	do	462	do	do	18.5
13	do	485	Female	do	39.0
13	do	482	Male	Ripe	40.0
13	do	484	Female	Unknown	57.0
13	do	517	Male	Ripe	54.0
13	do	465	Female	Unknown	48.0
13	do	466	Male	do	12.0
Dec. 15	Zamboanga, Mindanao.	521	do	Spawning	63.0
1948					
Jan. 7	West coast of Panay	510	do	Ripening	65.5
Feb. 23	Moro Gulf, Mindanao.	545	Female	Ripe	110.0
Feb. 25	Celebes Sea	446		Unknown	
Feb. 26	Davao Gulf, Mindanao.	490	Male	Ripe	51.0
26	do	458	do	Spawning	41.4
26	do	473	do	do	70.4
26	do	463	Female	Ripening	76.0
Feb. 27	do	513	Male	do	19.9
Feb. 29	do	429	do	do	33.4
29	do	441	Female	do	56.1
Mar. 3	Celebes Sea	445	do	do	53.5
3	do	438	do	do	37.0
3	do	461	Male	Ripe	39.0
3	do	431	do	do	23.0
Mar. 8	do	425	Female	Ripening	31.2
Mar. 9	do	431	do	do	40.0
9	do	455	Male	Spawning	73.0
9	do	453	do	do	48.5
9	do	437	do	Ripe	32.0
9	do	439	do	Spawning	44.0
9	do	438	do	Ripe	55.0
9	do	435	Female	Ripening	47.0
9	do	452	Male	Ripe	40.0
9	do	461	do	Spawning	63.0
Mar. 13	West coast of Panay	582	Female	do	142.0
13	do	569	Male	Ripe	96.1
13	do	567	do	do	52.2
13	do	546	Female	Spent	49.2
Mar. 19	Verde Island Passage, Luzon.	528	Male	Spawning	52.0
19	do	531	Female	do	69.5
Apr. 6	North Sulu Sea	607	do	Ripe	104.6
6	do	630	Male	do	76.6
6	do	573	do	Spawning	89.5
6	do	592	Female	Ripe	97.0
6	do	575	do	do	76.8
6	do	585	do	do	85.2
Apr. 10	Celebes Sea	495	do	do	48.5
Apr. 11	do	422	do	Spent	15.6
11	do	361	Male	Immature	3.0
11	do	382	do	do	3.9
11	do	372	do	do	1.1
11	do	375	Female	do	7.0
Apr. 13	do	469	do	Ripe	51.6
13	do	500	Male	do	28.9
13	do	460	do	Unknown	20.0
13	do	450	do	do	16.0
13	do	449	do	Spawning	27.9
13	do	448	Female	Ripe	44.5
13	do	390	Male	Immature	3.0
Apr. 15	Sulu Archipelago	445	Female	Ripe	52.5
15	do	426	do	do	36.5
15	do	469	Male	Spawning	45.5
Apr. 16	do	495	do	Ripe	31.0
16	do	520	do	do	58.7
16	do	493	do	Spawning	34.3

TABLE 6.—*Locality, length, sex, degree of maturity, and gonad weight of* Katsuwonus pelamis *taken in Philippine waters by the* Spencer F. Baird, *October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
Apr. 16	Sulu Archipelago	499	Male	Ripe	57.7
16	do	512	do	do	56.5
16	do	515	Female	do	64.5
16	do	505	Male	do	69.1
16	do	494	Female	do	45.1
16	do	504	Male	Spawning	81.5
16	do	509	Female	do	58.2
16	do	520	Male	Ripe	48.1
16	do	490	Female	do	73.0
Apr. 19	Basilan Island, Sulu Archipelago.	488	Male	do	40.8
19	do	510	do	do	42.2
19	do	487	do	Spawning	51.6
19	do	490	do	Ripe	59.1
19	do	520	Female	do	117.2
19	do	483	do	do	86.3
Apr. 20	do	513	Male	do	44.5
Apr. 21	West coast of Zamboanga Peninsula.	485	Female	do	64.0
21	do	564	Male	Ripening	36.6
21	do	542	Female	Ripe	91.5
21	do	514	do	do	104.0
21	do	505	Male	do	48.2
21	do	527	Female	do	83.3
May 4	Luzon Island	560	do	Ripening	177.5
May 6	West Coast of Zamboanga Peninsula.	510	do	Spawning	83
6	do	534	Male	do	50.3
May 9	Basilan Island, Sulu Archipelago.	549	do	Ripe	71.5
9	do	516	do	do	49.5
9	do	491	do	do	42.0
9	do	476	Female	Ripening	38.5
9	do	508	Male	Ripe	32.6
9	do	460	Female	Spent	23.7
9	do	493	do	Ripe	77.1
9	do	535	do	do	37.7
9	do	541	do	do	45.2
9	do	490	do	Spent	38.7
9	do	500	do	Ripe	35.8
9	do	485	do	Spent	34.5
9	do	495	Male	Ripening	27.3
9	do	510	Female	Spent	22.7
9	do	468	Male	Ripe	16.6
9	do	467	do	do	12.7
9	do	471	do	do	17.8
May 10	Sibuguey Bay, Moro Gulf.	498	Female	Spawning	60.9
10	do	445	Male	Ripe	17.5
10	do	441	do	do	17.7
May 11	North Moro Gulf	498	do	do	29.8
11	do	500	Female	Spawning	32.5
11	do	449	Male	Ripening	15.0
11	do	438	Female	do	22.1
11	do	429	Male	Ripe	15.2
11	do	459	Female	Spent	29.5
11	do	449	Male	Ripe	12.4
11	do	447	Female	Spent	22.4
11	do	413	Male	Ripe	29.7
May 12	Off Cotabato Province, Mindanao.	436	Female	Spent	26.9
12	do	422	Male	Ripe	33.2
12	do	402	Female	Spent	12.5
12	do	386	Male	Immature	.8
12	do	419	Female	Spent	22.4
12	do	388	Male	Ripening	8.3
12	do	359	(?)	Immature	1.5
12	do	493	Female	Ripe	90.0
12	do	490	do	do	70.0
May 14	Davao Gulf, Mindanao.	576	Male	Spawning	70.2
14	do	568	Female	do	92.5
May 15	do	463	Male	Ripe	37.0
15	do	484	do	do	38.5
15	do	471	Female	Spent	52.9
15	do	460	do	do	58.1
15	do	477	Male	Ripe	58.3
15	do	475	do	do	46.3
15	do	473	do	do	36.2
15	do	455	Female	Spawning	66.5
15	do	440	Male	Ripe	26.4
15	do	489	do	do	43.6
15	do	433	do	do	17.7
May 16	Celebes Sea	436	do	do	31.2
16	do	412	do	do	18.2

TABLE 6.—*Locality, length, sex, degree of maturity, and gonad weight of* Katsuwonus pelamis *taken in Philippine waters by the* Spencer F. Baird, *October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
May 16	Celebes Sea	422	Male	Spawning	5.0
May 20	West coast of Zamboanga Peninsula.	539	Female	Ripe	94.6
20	do	547	Male	do	83.9
May 22	North coast of Mindoro.	584	Female	do	122.1
June 14	Batangas, Luzon	505	do	do	69.2
June 15	East and south coast of Mindoro.	456	Male	do	30.2
15	do	481	Female	do	40.5
15	do	530	Male	Spawning	55.4
15	do	525	do	do	53.2
June 16	Southwest of Panay	575	Female	Ripe	59.8
16	do	535	do	do	63.9
16	do	532	Male	Spawning	31.0
16	do	525	Female	Spent	56.7
16	do	530	Male	Spawning	32.0
16	do	550	do	do	54.1
16	do	548	Female	Spent	89.0
16	do	597	do	do	208.5
June 18	Zamboanga Peninsula, Mindanao.	533	do	do	61.2
June 19	East Sulu Sea	529	Male	Spawning	50.0
19	do	503	do	Ripening	32.0
June 21	Dumarin Island, Palawan.	509	do	Ripe	19.0
21	do	505	do	Spent	22.5
21	do	485	do	do	32.0
21	do	522	Female	do	66.8
21	do	499	do	do	53.4
21	do	537	do	do	56.5
21	do	513	do	do	82.2
21	do	520	do	do	94.6
21	do	493	Male	Spawning	23.6
21	do	515	Female	Spent	48.4
21	do	553	do	do	56.5
21	do	483	Male	do	26.5
21	do	516	do	Spawning	31.0
21	do	547	do	Spent	43.5
21	do	538	Female	do	63.6
21	do	508	do	do	51.0
21	do	615	do	do	83.9
21	do	518	do	do	52.3
21	do	538	do	do	25.8
21	do	486	do	do	36.4
21	do	580	do	do	58.6
June 22	Tubbataha Reefs, Sulu Sea.	614	do	do	82.3
22	do	595	Male	Ripening	76.7
22	do	615	do	Spent	82.6
22	do	539	do	Ripe	28.0
22	do	560	Female	Spent	49.0
22	do	558	do	Ripening	8.2
22	do	555	Male	Ripe	33.2
22	do	553	Female	Spent	43.0
22	do	555	Male	Ripe	44.6
22	do	583	Female	do	103.8
22	do	574	do	Spent	50.5
22	do	551	do	do	46.8
22	do	570	Male	Ripe	73.0
22	do	621	do	do	58.5
22	do	605	Female	do	44.1
22	do	579	do	do	70.0
June 23	Puerto Princesa, Palawan.	535	do	Ripe	54.1
23	do	526	Male	Ripening	30.0
23	do	509	Female	Ripe	47.1
23	do	525	do	do	54.5
23	do	561	Male	do	35.0
23	do	564	do	do	36.0
23	do	545	do	do	60.6
23	do	565	do	do	38.2
23	do	553	Female	Ripening	5.1
23	do	546	do	Ripe	65.0
23	do	566	do	do	61.0
23	do	561	Male	do	33.5
23	do	530	do	do	54.0
23	do	576	do	Ripening	30.5
23	do	533	Female	Spent	60.0
23	do	535	do	Ripe	74.4
23	do	515	Male	do	43.0
23	do	507	Female	do	58.0

TABLE 6.—*Locality, length, sex, degree of maturity, and gonad weight of* Katsuwonus pelamis *taken in Philippine waters by the* Spencer F. Baird, *October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
June 23	Puerto Princesa, Palawan.	516	Female	Ripe	51.0
23	do	519	Male	do	25.0
23	do	530	do	do	36.2
23	do	531	do	do	32.8
23	do	505	do	do	36.0
June 24	West Sulu Sea	584	Female	Spent	55.8
24	do	510	Male	Ripe	41.2
24	do	578	do	Spent	27.3
24	do	580	Female	do	57.2
June 25	East Sulu Sea	525	Male	Ripe	50.0
June 27	North Sulu Sea	563	Female	Spent	58.5
27	do	540	do	Ripe	40.5
June 29	Busuanga Islands, China Sea.	488	do	do	51.7
29	do	488	do	do	45.0
29	do	458	do	do	66.5
29	do	468	Male	do	15.6
29	do	466	Female	do	42.0
29	do	492	Male	do	55.0
July 10	South Sulu Sea	504	Female	do	45.0
10	do	498	Male	do	35.1
10	do	508	Female	do	37.4
10	do	510	Male	Spawning	46.8
July 11	do	551	do	Ripe	81.5
11	do	508	do	do	70.0
July 14	Balabac Island, Sulu Sea.	508	do	do	41.3
14	do	458	Female	do	63.5
14	do	457	do	do	50.0
14	do	345	Male	Spawning	31.0
14	do	340	Female	Ripe	33.5
July 17	West coast of Zamboanga Peninsula.	565	Male	Spawning	34.5
17	do	588	Female	Ripe	98.5
July 18	West coast of Panay.	528	do	do	84.0
18	do	516	Male	do	25.0
July 27	North Sulu Sea	565	do	do	36.3
27	do	554	do	Spawning	43.6
27	do	535	do	do	41.0
27	do	516	Female	Ripe	51.2
27	do	540	Male	Spawning	37.0
27	do	564	do	do	67.2
27	do	518	do	do	30.5
27	do	643	do	do	100.0
27	do	627	Female	Ripe	150.5
27	do	615	Male	Spawning	94.0
July 29	Zamboanga, Mindanao.	481	do	Ripe	21.0
29	do	472	do	do	29.5
29	do	476	do	Spawning	32.5
29	do	500	Female	Spent	39.0
29	do	478	Male	Ripe	32.3
29	do	478	do	Spawning	39.5
29	do	448	do	Ripe	29.0
29	do	440	Female	do	29.0
29	do	436	Male	Spawning	18.0
29	do	448	Female	Ripe	27.0
July 30	Sulu Archipelago	453	Male	do	33.2
30	do	416	do	do	14.7
30	do	452	Female	do	35.6
30	do	405	do	do	67.7
Aug. 1	Northeast coast of Borneo.	420	do	Ripening	14.2
Aug. 2	Southwest Celebes Sea.	431	do	do	25.0
2	do	401	do	do	11.8
2	do	396	do	do	14.0
Aug. 6	do	465	Male	Ripe	48.0
6	do	440	do	Spawning	28.5
6	do	442	Female	Spent	34.5
6	do	440	Male	Spawning	28.0
Aug. 10	Sibuguey Bay, Moro Gulf.	519	do	Ripe	28.0
10	do	486	Female	do	37.0
10	do	521	do	do	66.0
10	do	488	do	do	34.0
10	do	481	Male	do	29.0
Aug. 11	Northeast Sulu Sea	580	Female	do	87.0
11	do	608	Male	do	70.0
11	do	580	do	do	67.0
11	do	577	do	do	65.0
Aug. 31	South Sibuyan Sea	584	do	do	60.0

TABLE 6.—*Locality, length, sex, degree of maturity, and gonad weight of* Katsuwonus pelamis *taken in Philippine waters by the* Spencer F. Baird, *October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
Sept. 4	North Moro Gulf	456	Female	Spent	55.5
Sept. 13	Celebes Sea	460	do	Ripe	43.0
13	do	466	do	do	82.0
13	do	465	do	do	49.0
Nov. 4	North Palawan	498	do	Spent	54.0
4	do	475	Male	Spawning	24.0
4	do	495	Female	Ripe	40.0
Nov. 6	Northeast Palawan	510	do	do	50.0
6	do	498	Male	Spawning	54.0
Nov. 7	East coast of Palawan	525	do	do	53.0
Nov. 10	do	430	Female	Ripe	20.0
10	do	410	Male	do	10.0
10	do	417	do	do	6.0
10	do	465	Female	do	30.0
10	do	415	Male	do	4.0
10	do	430	Female	do	20.0
Nov. 13	South Sulu Sea	515			
Nov. 15	do	433	Male	Ripening	4.0
15	do	464	do	Ripe	8.0
Nov. 20	Northeast Sulu Sea	490			18.0
20	do	470	Female	Ripe	14.0
20	do	480	Male	do	10.0
Nov. 21	North Sulu Sea	510	Female	do	40.0
Nov. 22	do	495	Male	Spawning	30.0
22	do	488	Female	Ripe	40.0
Nov. 23	West coast of Mindoro.	495	do	Ripening	40.0

The most of the other individuals of this species in the collection were considered to be ripening. Ripening individuals were found throughout the year but most abundantly from April through August. Only a few ripe specimens were taken in the course of the operations and no spawning or spent fish were captured. Although the sample is not sufficiently adequate to form the basis for conclusions regarding spawning, it appears that as scattered specimens of ripe fish are found over a long period of time the spawning period is an extended one. On the basis of the present data the spawning period seems to be most intense during May, June, July, and August.

TABLE 7.—*Monthly summary of all specimens of troll-caught* Neothunnus macropterus, *taken by the* Spencer F. Baird, *October 1947–November 1948*

Month	Immature	Ripening	Ripe	Spawning	Spent	Unknown	Total
ALL FISH							
October							
November							
December	6	25	1			2	34
January	3		1			1	5
February		2					2
March		2	1			9	12
April	2	11				11	24
May	24	4	1			12	41
June	4	37	6			1	48
July	2	6	1			14	23
August	4	16	2			13	35
September		2	2			8	12
October							
November		3					3
Total	45	108	15			71	239
MALES							
October							
November							
December	3	14	1				18
January	1		1				2
February							
March			1				1
April	2	6					8
May	13	2	1				16
June	3	20	4				27
July	1	3	1				5
August	2	8	2				12
September		1	2				3
October							
November							
Total	25	54	13				92
FEMALES							
October							
November							
December	3	11					14
January	2						2
February		2					2
March		2					2
April		5					5
May	11	2					13
June	1	17	2				20
July	1	3					4
August	2	8					10
September		1					1
October							
November		3					3
Total	20	54	2				76

TABLE 8.—*Length-frequency at several stages of gonad development of* Neothunnus macropterus *from the Philippines and the northern Marshall Islands* [1]

Length in millimeters	Immature					Ripening				Ripe				Spent			
	Philippines	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands
	Sex ?	Male	Male	Female	Female	Male	Male	Female	Female	Male	Male	Female	Female	Male	Male	Female	Female
340–359	1																
360–379	1																
380–399	2																
400–419	5												None		None		
420–439	7													None		None	
440–459	13																
460–479	18	1		2													
480–499	10	9		6													
500–519	6	5	2	8		1		1									

See footnote at end of table.

TABLE 8.—*Length-frequency at several stages of gonad development of* Neothunnus macropterus *from the Philippines and the northern Marshall Islands* [1]—Continued

Length in millimeters	Immature					Ripening				Ripe				Spent			
	Philippines	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands	Philippines	Marshall Islands
	Sex ?	Male	Male	Female	Female	Male	Male	Female	Female	Male	Male	Female	Female	Male	Male	Female	Female
520–539	6	6	11	1	1	7	1	4		1	1						
540–559		2	16	1	3	10	1	10		3							
560–579		1	9		1	4		4									
580–599			3	1	2	6	1	4		1							
600–619	2		7			5		9		3							
620–639			6		3	5		4									1
640–659		1	1	1	5	6		4			5						
660–679			5		2	3	2	3	1	2	2						
680–699			4		4	2		4									
700–719			3			4		2	2	1		2					
720–739			2		1		1			1							
740–759			2		1			1									
760–779			2			1	1	1									
780–799					2		1	2									
800–819			1			1		1									
820–839						1				1							3
840–859			2						1		1						
860–879					2												
880–899											1						1
900–919					1												
920–939							2		1								1
940–959							1		1								
960–979									1								
980–999									1								
1,000–1,019							1				1						
1,020–1,039																	
1,040–1,059																	1
1,060–1,079									1								
1,080–1,099											1						
1,100–1,119																	
1,120–1,139																	
1,140–1,159																	
1,160–1,179											1						
1,180–1,199																	
1,200–1,219																	
Total	71	25	76	20	28	54	12	54	9	13	13	2	0	0	0	0	7

[1] Length-frequency data of Marshall Islands specimens taken from Marr (1948).

TABLE 9.—*Locality, length, sex, degree of maturity, and gonad weight of* Neothunnus macropterus *taken in Philippine waters by the* Spencer F. Baird, *October 1947–November 1948*

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1947					
Dec. 11	Sibutu Passage, Sulu Archipelago.	673	Female	Ripening	131.4
11	do	575	Male	do	21.9
11	do	520	do	do	12.0
11	do	560	do	do	15.6
11	do	608	do	Ripe	85.9
11	do	601	do	Ripening	33.0
11	do	601	do	do	40.0
11	do	512	Female	Immature	8.0
11	do	700	Male	Ripening	94.0
11	do	645	do	do	70.0
11	do	595	do	do	63.3
11	do	610	Female	do	99.2
Dec. 12	do	568	do	do	52.0
12	do	574	Male	do	32.5
12	do	523	do	Immature	3.5
12	do	554	Female	Ripening	26.5
12	do	575	do	do	22.2
12	do	612	do	do	74.8
12	do	555	do	do	14.4
12	do	547	do	do	48.6
12	do	468	do	do	58.5
12	do	546	Male	do	31.5
12	do	621	do	do	66.5
12	do	480	Unknown	Immature	2.3
12	do	590	Male	Ripening	38.2
12	do	626	do	do	35.7

[1] Gonad weight less than 1 gram.

TABLE 9.—*Locality, length, sex, degree of maturity, and gonad weight of* Neothunnus macropterus *taken in Philippine waters by the* Spencer F. Baird, *October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1947					
Dec. 12	Sibutu Passage, Sulu Archipelago.	553	Male	Ripening	46.1
12	do	527	Female	Immature	4.6
12	do	517	do	do	8.0
12	do	520	Unknown	do	2.4
12	do	526	Male	do	8.0
12	do	510	do	do	5.5
Dec. 16	Basilan Island, Sulu Archipelago.	596	Female	Ripening	54.0
16	do	602	do	do	12.0
1948					
Jan. 12	Sulu Archipelago	583	Unknown	Immature	3.0
12	do	612	Male	Ripe	13.5
12	do	587	Female	Immature	6.8
12	do	546	do	do	7.8
12	do	545	Male	do	4.2
Feb. 19	Port Santa Maria, Zamboanga Peninsula.	797	Female	Ripening	72.1
19	do	785	do	do	58.3
Mar. 4	Celebes Sea	604	do	do	106.0
4	do	587	do	do	76.2
4	do	525	Male	Ripe	38.0
Mar. 8	do	470	Unknown	Immature	(1)
8	do	455	do	do	
8	do	352	do	do	

TABLE 9.—*Locality, length, sex, degree of maturity, and gonad weight of* Neothunnus macropterus *taken in Philippine waters by the* Spencer F. Baird, *October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
Mar. 14	Verde Island Passage, Luzon.	480	Unknown	Immature	
14	do	453	do	do	
14	do	463	do	do	
14	do	478	do	do	
14	do	482	do	do	
14	do	473	do	do	
Apr. 11	Celebes Sea	454	do	do	
11	do	450	do	do	
11	do	449	do	do	
Apr. 12	do	493	Male	do	2.0
12	do	426	Unknown	do	1.9
12	do	433	do	do	2.6
Apr. 13	do	614	Female	Ripening	74.4
13	do	464	Unknown	Immature	1.5
13	do	556	Female	Ripening	61.5
13	do	593	Male	do	31.2
13	do	558	do	do	48.3
13	do	418	Unknown	Immature	1.0
Apr. 14	do	492	do	do	2.2
14	do	470	do	do	1.4
14	do	472	do	do	2.0
14	do	477	Male	do	3.8
Apr. 17	Sulu Archipelago	631	do	Ripening	14.1
17	do	630	Female	do	19.1
17	do	530	Male	do	8.5
Apr. 18	do	600	do	do	7.5
Apr. 19	Basilan Island	596	Female	do	12.4
19	do	665	do	do	17.3
Apr. 21	West coast of Zamboanga Peninsula.	501	Unknown	Immature	2.3
21	do	537	Male	do	8.1
May 6	do	526	Unknown	do	2.5
6	do	521	Male	do	3.5
May 9	East coast Zamboanga.	485	do	do	2.1
9	do	478	Female	do	2.1
9	do	492	Unknown	do	2.0
9	do	517	Male	do	2.1
9	do	517	Female	do	2.3
9	do	769	do	Ripening	103.4
9	do	665	Male	do	42.9
9	do	608	Female	do	48.3
May 10	North Moro Gulf	531	Male	Immature	3.5
10	do	672	do	Ripe	63.8
May 12	East Moro Gulf	483	Female	Immature	2.4
12	do	514	do	do	2.9
12	do	488	Male	do	2.3
12	do	516	do	Ripening	12.0
12	do	418	Unknown	Immature	1.3
12	do	496	Male	do	2.0
12	do	484	do	do	2.0
12	do	507	Female	do	2.8
12	do	491	do	do	4.5
12	do	497	do	do	1.6
12	do	461	Unknown	do	2.3
12	do	485	Male	do	2.4
12	do	409	Unknown	do	1.9
12	do	472	Female	do	2.2
12	do	497	do	do	2.0
12	do	487	Male	do	2.2
12	do	484	Unknown	do	1.4
12	do	503	Female	do	5.0
12	do	512	Unknown	do	1.9
12	do	593	Male	Ripening	20.9
12	do	505	Unknown	Immature	2.5
12	do	504	Male	do	6.0
12	do	475	Unknown	do	2.3
12	do	528	do	do	2.0
12	do	492	Female	do	5.5
12	do	479	Unknown	do	2.2
12	do	488	Male	do	1.6
May 15	Davao Gulf, Mindanao.	491	do	do	1.8
May 22	Mindanao Sea	526	Unknown	do	1.0
22	do	533	Male	do	4.2
June 17	East Sulu Sea	513	do	do	2.5
17	do	524	do	Ripening	8.2
June 18	West coast of Zamboanga Peninsula.	520	do	Immature	2.5
18	do	732	do	Ripe	65.0
18	do	612	do	Ripening	16.4
June 22	Tubbataha Reefs, Sulu Sea.	800	Female	do	47.0
22	do	745	do	do	77.2

TABLE 9.—*Locality, length, sex, degree of maturity, and gonad weight of* Neothunnus macropterus *taken in Philippine waters by the* Spencer F. Baird, *October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
June 23	East coast of Palawan	828	Male	Ripe	52.3
23	do	674	do	Ripening	30.0
23	do	683	Female	do	25.3
23	do	660	do	do	25.0
23	do	618	do	do	10.5
23	do	650	Male	do	43.9
23	do	662	do	do	11.6
23	do	640	do	do	10.0
23	do	657	do	do	7.5
23	do	651	Female	do	32.5
23	do	700	do	Ripe	85.7
23	do	668	Male	do	21.5
23	do	710	Female	do	54.6
23	do	622	do	Ripening	22.6
23	do	656	do	do	86.2
23	do	715	Male	do	32.1
23	do	708	do	Ripe	55.0
23	do	697	do	Ripening	17.0
23	do	656	do	do	14.0
23	do	696	Female	do	37.2
23	do	613	do	do	11.5
23	do	630	do	do	18.0
23	do	641	do	do	21.0
23	do	597	Male	do	11.0
23	do	627	do	do	9.0
23	do	646	Female	do	20.0
23	do	604	Male	Ripening	65.0
23	do	652	do	Immature	4.0
23	do	700	do	Ripening	17.0
23	do	643	do	do	18.0
23	do	640	Female	Immature	3.0
23	do	596	Unknown	do	
June 24	West Sulu Sea	716	Female	Ripening	32.5
24	do	682	do	do	25.5
24	do	711	Male	do	10.5
24	do	800	do	do	60.0
24	do	828	do	do	43.0
24	do	769	do	do	40.0
24	do	618	Female	do	27.4
June 27	Cuyo Islands, Sulu Sea.	683	do	do	44.0
27	do	689	Male	do	60.5
July 12	Southwest Sulu Sea	531	Unknown	Immature	
July 16	South Sulu Sea	462	do	do	
16	do	457	do	do	
July 17	West coast of Zamboanga Peninsula.	550	Male	Ripening	5.1
17	do	518	Female	Immature	2.5
17	do	554	Male	Ripening	6.2
17	do	520	do	Immature	3.6
17	do	522	Female	Ripening	9.0
17	do	455	Unknown	Immature	
July 27	Northeast Sulu Sea	385	do	do	
27	do	422	do	do	
July 29	Basilan Island, Sulu Archipelago.	531	Female	Ripening	12.0
29	do	481	Unknown	Immature	
29	do	437	do	do	
29	do	397	do	do	
29	do	406	do	do	
29	do	585	Male	Ripening	14.5
29	do	505	Unknown	Immature	
July 30	Sulu Archipelago	475	do	do	
30	do	532	Female	Ripening	42.2
30	do	617	Male	Ripe	42.5
30	do	451	Unknown	Immature	
30	do	458	do	do	
Aug. 1	Northeast coast of Borneo, Celebes Sea.	430	do	do	
1	do	459	do	do	
Aug. 3	West Celebes Sea	438	do	do	
Aug. 4	do	461	do	do	
4	do	458	do	do	
4	do	428	do	do	
Aug. 6	do	546	Female	Ripening	39.3
6	do	540	do	do	29.1
6	do	535	Male	do	26.2
Aug. 7	Basilan Island, Mindanao.	585	do	Ripe	40.0
7	do	516	Female	Ripening	7.0
7	do	563	Male	do	8.5
7	do	536	Female	do	7.0
7	do	527	Male	do	7.5
7	do	537	do	do	5.0

TABLE 9.—*Locality, length, sex, degree of maturity, and gonad weight of* Neothunnus macropterus *taken in Philippine waters by the* Spencer F. Baird, *October 1947–November 1948*—Continued

Date	Locality	Fork length in millimeters	Sex	Degree of maturity	Gonad weight in grams
1948					
Aug. 7	Basilan Island, Mindanao.	487	Female	Immature	4.5
7	do	476	Unknown	do	
7	do	518	Female	do	4.0
7	do	504	Male	do	3.0
7	do	454	Unknown	do	
7	do	502	do	do	
7	do	476	do	do	
7	do	464	do	do	
Aug. 10	Zamboanga, Mindanao.	472	do	do	
10	do	567	Female	Ripening	10.5
10	do	544	Male	Immature	4.5
10	do	550	do	Ripening	6.0
10	do	545	do	do	6.5
10	do	554	do	do	7.0
10	do	551	do	do	29.0
10	do	555	Female	do	10.5
10	do	573	do	do	13.0
10	do	522	Unknown	Immature	
10	do	554	Female	Ripening	7.0
10	do	548	Male	Ripe	26.0
Sept. 3	West coast of Zamboanga Peninsula	565	do	Ripening	7.0
Sept. 4	North Moro Gulf	454	Unknown	Immature	
4	do	464	do	do	
4	do	481	do	do	
4	do	497	do	do	
4	do	480	do	do	
4	do	460	do	do	
4	do	371	do	do	
Sept. 6	Sarangani Island, Sulu Archipelago.	543	Female	Ripening	17.0
6	do	555	Male	Ripe	18.5
6	do	552	do	do	15.5
6	do	406	Unknown	Immature	
Nov. 16	South Sulu Sea	550	Female	Ripening	14.0
16	do	620	do	do	16.0
16	do	580	do	do	11.0

SUMMARY

The data for these preliminary observations on the spawning of tuna in Philippine waters were collected aboard the Philippine Fishery Program's research vessel *Spencer F. Baird* from October 1947 through November 1948. Three species of tuna, *Neothunnus macropterus*, *Katsuwonus pelamis*, and *Euthynnus yaito*, were collected in numbers sufficient to make several tentative observations relative to their spawning. The gross field method used in determining the degree of sexual maturity, although satisfactory for preliminary exploratory studies, needs considerable refinement before it can be used in a comprehensive study of the life histories of the several species.

Euthynnus yaito, in all stages of sexual maturity, was noted throughout the period, and was the most abundant species taken during these studies. The sample was not sufficiently adequate to determine accurately if spawning remains fairly constant throughout the year or if a peak or several peaks of intensive spawning occur followed by periods in which only a few scattered individuals spawn. On the basis of the available data the former seems likely.

The second most abundant species taken was *Katsuwonus pelamis*. Both males and females in all degrees of sexual maturity were taken throughout the year. The data indicate that spawning of greater intensity occurs during April, May, June, and July than the rest of the year.

The collection of *Neothunnus macropterus* furnished little data on the spawning habits of this species as almost one-half of the fish caught were immature and most of the others taken were in the early stages of ripening. Only a few individuals were taken that were classified as ripe and no spawning or spent fish were caught. Scattered specimens of ripe males were taken at random intervals throughout the year, and two ripe females were taken in June. Data based upon ripening fish and a few ripe individuals indicate that spawning apparently extends over a considerable period but is most intense during May, June, July, and August.

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FISH AND WILDLIFE SERVICE, ALBERT M. DAY, *Director*

BIOMETRIC COMPARISON BETWEEN YELLOWFIN TUNAS (*NEOTHUNNUS*) OF ANGOLA AND OF THE PACIFIC COAST OF CENTRAL AMERICA

BY MILNER B. SCHAEFER AND LIONEL A. WALFORD
Aquatic Biologists

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BIOMETRIC COMPARISON BETWEEN YELLOWFIN TUNAS (*NEOTHUNNUS*) OF ANGOLA AND OF THE PACIFIC COAST OF CENTRAL AMERICA

By MILNER B. SCHAEFER and LIONEL A. WALFORD, *Aquatic Biologists*

The several species of fishes commonly called tuna are characteristically widely distributed and probably generally composed of many populations. The determination of the identity of these populations is fundamental to understanding the biology of tunas. This can be accomplished only by extensive biometric comparison between samples of tunas taken throughout the range of their distribution.

During November 1948 one of us (Walford) had occasion to visit the Port of Mossamedes in Angola (Portuguese West Africa) which is the center of a growing tuna-canning industry. Through the kindness of Capt. Josina Da Costa, of Lisbon, Portugal, he was able to visit canneries where tuna were being packed, to go out on a fishing vessel, and to make a number of measurements and counts on freshly caught specimens of yellowfin tuna. The opportunity to gather these data was particularly gratifying because it meant that measurement data could be collected exactly comparable with those available for Pacific yellowfin tuna, thus making possible a detailed comparison of the morphometric characteristics of the two. Such a comparison will be, we hope, a valuable contribution to the solution of the problems of speciation of the tunas.

Measurements and counts were made of various characters on 60 yellowfin tuna selected to cover as evenly as possible the size range of available specimens. Measurements were made in millimeters in accordance with the methods employed by American researchers studying Pacific tunas (Schaefer 1948; Marr and Schaefer 1949). Although slide calipers of the type employed by those authors were not available, exactly comparable measurements were made by the use of large dividers and a millimeter scale. The basic original data are tabulated in table 1.

The many detailed computations in this paper were performed by Mr. Kalfred Yee, whose assistance is gratefully acknowledged.

RELATIVE GROWTH OF ATLANTIC YELLOWFIN TUNA

Morphometric data on tunas, like those on other fishes, following the methodology of classical taxonomy, have usually been recorded in terms of body proportions, that is, the number of times one dimension is contained in another. The committee of experts for the examination of scientific methods applied to the study of tunas, which met in Madrid and Cadiz in 1932, for example, (Anonymous 1933) recommended the employment of various "indices biométriques" which are ratios of one body dimension to another. In this they followed the usage of Frade (1929, 1931) and Heldt (1931) who were members of the committee and who had employed similar indices in studies of Mediterranean and Atlantic tunas. Both of these authors have employed such indices to compare tunas of the same species from different regions. Jordan and Evermann (1926) and Nichols and LaMonte (1941) have employed body proportions in characterizing species, as have Godsil and Byers (1944) in their painstaking study of Pacific tunas.

Body proportions are, in general, not satisfactory for comparing tunas of different sizes, because the differential growth of different body parts causes the value of a proportion to change as the fish grows. Only when no differential growth exists between the parts whose dimensions are used in computing the ratio, that is, only when there is a constant ratio between the dimensions of such parts, can the average value of such a ratio be used to compare fish of different sizes. Where the ratio does not remain constant as the fish grows, it is necessary to compare only fish of the same size or to compare the regressions of one dimension on another. Schaefer (1948) computed such regressions to characterize the yellowfin tuna (*N. macropterus*) from the Pacific Ocean off Central America, employing linear regressions, or

TABLE 1.—*Morphometric data from 60 specimens of Yellowfin tuna (Neothunnus albacora) from the commercial catch at Mossamedes, Angola, Nov. 12–15, 1948*

Total length	Head length	Snout to insertion first dorsal	Snout to insertion second dorsal	Snout to insertion anal	Snout to insertion ventral	Greatest depth	Length pectoral	Pectoral insertion to insertion first dorsal	Length base first dorsal	Length base second dorsal	Spread caudal	Length longest dorsal spine	Length first dorsal spine	Length second dorsal	Length anal	Length longest dorsal finlet	Diameter of iris	Length maxillary	Least depth caudal peduncle	Greatest width caudal peduncle at keels	Number of first dorsal spine	Number of dorsal finlets	Number of anal finlets	Number of gill rakers	Sex
Nov. 12																									
751	205	240	417	455	231	184	214	116	186	68	230	86	86	108	111	19	28	80	19	62	14	8+1	8+1	9+21	M
1536	400	442	766	846	430	409	373	241	343	125	590	180	180	450	491	51	45	152	40	(?) 157	13	9+1	8+1	9+21	M
1298	323	367	651	719	360	319	338	190	296	104	432	147	147	254	273	43	33	128	32	135	14	8+1	8+1	10+20	M
1626	416	464	835	903	463	436	417	249	391	130	605	189	189	445	454	57(4th)	37	153	46	154	14	8+1	6+1	9+22	M
1600	405	435	812	901	449	456	404	249	398	136	-----	189	189	426	505	58(4th)	44	156	43	153	14	9	8+1	9+22	M
1299	344	365	647	721	375	343	346	189	305	106	449	161	161	318	367	44(6th)	38	135	35	117	14	8+1	8+1	8+20	F
844	243	250	459	516	269	222	251	127	214	70	230	102	102	137	130	28(4th)	30	96	22	65	14	9	8+1	9+21	M
1318	350	376	677	741	388	335	348	197	311	108	487	162	162	344	355	45(4th)	39	128	33	138	14	9	9	10+21	F
1577	404	438	793	970	445	409	372	231	379	141	555	185	185	402	461	50(4th)	40	155	41	148	14	9	9	11+21	M
Nov. 13																									
1193	310	336	615	673	345	318	321	194	285	95	396	130	130	238	250	35(4th)	36	120	29	117	13	9+1	9	8+21	F
1406	361	391	705	769	397	360	327	215	323	121	453	143	143	297	327	46(4th)	37	141	33	137	14	9+1	9	10+22	M
1437	376	401	735	796	418	390	371	216	347	116	524	167	167	353	407	48(5th)	36	138	37	135	14	9	8+1	9+20	M
1276	344	369	659	716	373	307	318	176	310	102	447	156	156	289	292	43(4th)	38	128	31	126	14	9	9	9+20	F
1373	346	386	690	758	389	350	338	210	330	104	457	144	144	339	363	46(4th)	39	129	33	132	14	9	9	9+21	F
1338	347	370	675	744	385	362	347	190	318	106	490	152	152	296	332	42(4th)	37	125	34	129	14	9	9	10+21	M
1371	360	381	695	760	382	344	354	196	332	107	480	171	171	347	400	46(5th)	37	133	37	125	14	8+1	9	9+20	F
1381	353	391	701	750	384	362	344	200	342	93	471	149	149	398	335	45(4th)	38	133	33	141	14	9	9	9+21	M
1166	310	339	604	661	348	298	339	174	293	91	390	125	125	233	227	40(4th)	34	115	29	110	14	8+1	8+1	9+21	M
491	160	167	279	316	179	145	131	76	123	45	153	55	55	43	44	14(4th)	27	58	11	30	15	8+1	8+1	9+19	-----
Nov. 14																									
769	223	248	442	482	250	-----	236	-----	205	-----	-----	-----	-----	113	117	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
805	230	256	455	485	260	-----	224	-----	204	-----	-----	-----	-----	132	137	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
797	220	242	427	479	255	-----	230	-----	194	-----	-----	-----	-----	124	118	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
831	243	255	454	505	262	-----	242	-----	214	-----	-----	-----	-----	118	124	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1172	313	325	595	665	349	-----	348	-----	288	-----	-----	-----	-----	238	269	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
828	238	265	446	500	256	-----	233	-----	188	-----	-----	-----	-----	135	112	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
787	226	244	434	482	246	-----	220	-----	198	-----	-----	-----	-----	119	128	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
799	226	250	436	476	252	-----	230	-----	200	-----	-----	-----	-----	113	120	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
807	225	248	428	485	256	-----	220	-----	217	-----	-----	-----	-----	196	124	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
790	225	247	435	483	252	-----	220	-----	197	-----	-----	-----	-----	121	124	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
830	238	261	455	508	263	-----	225	-----	204	-----	-----	-----	-----	116	120	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
826	230	250	456	493	265	-----	225	-----	198	-----	-----	-----	-----	132	131	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1114	289	328	584	624	330	-----	289	-----	162	-----	-----	-----	-----	197	207	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
985	264	290	513	572	291	-----	268	-----	235	-----	-----	-----	-----	154	157	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
802	220	262	452	480	251	-----	219	-----	201	-----	-----	-----	-----	118	122	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
789	217	243	435	471	241	-----	220	-----	203	-----	-----	-----	-----	118	119	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1170	309	337	612	672	350	-----	315	-----	294	-----	-----	-----	-----	240	241	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1183	316	338	608	672	339	-----	327	-----	281	-----	-----	-----	-----	262	283	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1254	327	349	649	720	358	-----	326	-----	306	-----	-----	-----	-----	286	311	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1448	356	395	736	816	414	-----	345	-----	351	-----	-----	-----	-----	326	277	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1200	320	350	618	684	358	-----	329	-----	286	-----	-----	-----	-----	(1)	345	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1364	357	371	691	772	395	-----	360	-----	327	-----	-----	-----	-----	373	423	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1194	318	336	620	694	349	-----	332	-----	294	-----	-----	-----	-----	243	257	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1133	299	323	589	647	337	-----	321	-----	280	-----	-----	-----	-----	210	248	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1180	309	335	613	671	349	-----	313	-----	290	-----	-----	-----	-----	256	278	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1207	315	342	614	686	345	-----	320	-----	289	-----	-----	-----	-----	229	263	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1255	328	354	648	716	367	-----	356	-----	303	-----	-----	-----	-----	300	316	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1286	332	356	666	733	380	-----	353	-----	315	-----	-----	-----	-----	328	356	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1468	378	408	757	828	420	-----	372	-----	358	-----	-----	-----	-----	531	570	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Nov. 15																									
1372	350	376	704	777	393	-----	349	-----	335	-----	-----	-----	-----	303	290	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1365	361	375	695	764	401	-----	347	-----	327	-----	-----	-----	-----	290	345	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1324	339	373	674	754	386	-----	339	-----	316	-----	-----	-----	-----	285	301	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1421	350	386	715	773	389	-----	362	-----	350	-----	-----	-----	-----	367	388	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1430	371	416	720	794	412	-----	392	-----	333	-----	-----	-----	-----	385	439	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
791	226	249	425	475	256	-----	219	-----	194	-----	-----	-----	-----	123	132	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
793	227	235	420	480	248	-----	231	-----	193	-----	-----	-----	-----	111	115	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
809	230	242	449	483	254	-----	230	-----	214	-----	-----	-----	-----	129	130	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
810	240	248	438	488	250	-----	221	-----	193	-----	-----	-----	-----	122	122	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
789	226	240	434	475	247	-----	226	-----	193	-----	-----	-----	-----	136	120	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
798	223	245	450	472	244	-----	222	-----	207	-----	-----	-----	-----	120	120	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
823	231	244	445	473	252	-----	235	-----	203	-----	-----	-----	-----	141	131	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----

[1] Broken.

transformations which yield linear regressions. Godsil (1948) employed a generalized formula which would fit both linear and curvilinear regressions to describe the growth of head length and the distances from snout to each fin insertion in relation to body length of *N. macropterus*, and also for a number of body proportions of albacore (*Thunnus germo*).

In this study we have followed Schaefer (1948). We have computed the linear mean square regressions for the original data where the variables have a linear relationship, and where they were found to have a nonlinear relationship we have employed a transformation that yields a linear relationship between the new variables. The statistics describing the various regressions, together with the sums of squares and products of deviations about the means, are tabulated in table 2. The sums of squares and products of deviations about the means are included for the convenience of other workers desiring to compare similar data with ours by means of covariance analysis. In figures 1 to 15 are plotted various regressions, together with similar regressions from Schaefer's Costa Rican data.

A linear relationship between the original variables was evident for each regression except length of anal fin on total length, length of second dorsal fin on total length, and length of pectoral fin on total length. Except in these three cases, the rate of increase of the dimension in question remains proportional to the rate of increase in total length, over the size range considered. The second dorsal and anal fins grow much faster than the body, and the rate of growth relative to rate of growth of total length also increases with size of fish. The rate of growth of the pectoral fin relative to rate of growth of total length decreases as the size of the fish increases.

Although with the three exceptions noted there appears to be a linear relationship between the variables, the ratio of one dimension to another does not in most cases remain constant since the y intercepts of the linear-regression lines are different from zero, in which cases the ratios in question will change with size of fish. However, the regression of greatest body depth on total length has a y intercept that does not differ significantly from zero; the same result was found for Costa Rican yellowfin. Similarly, for both the African and the Costa Rican yellowfin, the y intercept of the regression of longest (first) dorsal ray on total length does not differ significantly from zero. The regression of distance from pectoral insertion to insertion of first dorsal on total length for African yellowfin has a y intercept not differing significantly from zero; in the case of Costa Rican fish this regression was found to differ significantly from zero, but so slightly that expression of the dependent variable as a percentage of total length would result in a negligibly small error. The length of base of first dorsal, the regression of which on total length for Costa Rican fish was found to have a y intercept only slightly different from zero, differs from zero in the case of African fish to the extent that the ratio of the dimensions in question would change appreciably with size of fish.

TABLE 2.—*Statistics describing regressions of body proportions of yellowfin tuna from Angola*

Independent variable x	Dependent variable y	N	$\bar{x}$	$\bar{y}$	Sx^2	Sy^2	Sxy	b	$s_{y.x}$	a
Total length	Head length	60	1113.6	297.03	4777250	241246	1069271	.2238	5.73	47.8
Do	Snout to insertion first dorsal	60	1113.6	322.4	4777250	282829	1155796	.2419	7.42	67.0
Do	Snout to insertion second dorsal	60	1113.6	580.9	4777250	1008031	2189648	.4584	8.49	70.4
Do	Snout to insertion anal	59	1105.8	634.8	4558918	1154267	2289060	.5021	9.35	79.6
Do	Snout to insertion ventral	60	1113.6	329.7	4777250	294313	1181866	.2474	5.78	54.2
Do	Greatest body depth	19	1274.8	334.2	1562973	115626	418487	.2678	14.5	−7.2
Do	Pectoral insertion to insertion first dorsal	19	1274.8	191.4	1562973	36004	233649	.1495	7.96	0.80
Do	Length base first dorsal	59	1113.6	271.2	4777250	251797	1089396	.2280	7.62	17.3
Do	Spread caudal	18	1256.7	435.5	1451335	252568	594723	.4098	23.5	−79.5
Do	Length longest (first) dorsal spine	19	1274.8	147.0	1562973	22576	182003	.1164	9.01	−1.45
Do	Length longest dorsal finlet	19	1274.8	42.1	1562973	2296	58791	.0376	2.24	−5.83
Log total length	Length pectoral fin	60	3.0317	297.2	0.822463	245933	441.9995	537.4	12.0	-------
Do	Log length second dorsal fin	58	3.0330	2.3240	0.804606	2.977096	1.524508	1.895	.0398	-------
Do	Log length anal fin	60	3.0317	2.3415	0.822463	3.443019	1.651653	2.008	.0467	-------
Length second dorsal fin	Length anal fin	58	239.0	253.2	739047	931501	817109	1.106	22.4	−11.0
Length of head	Diameter of iris	19	334.6	36.5	81785	384.7	4971.8	.0608	2.20	16.1
Do	Length of maxillary	19	334.6	126.5	81785	11509	30356	.3712	3.77	2.28

Logarithms are to the base 10
N=number of specimens
$\bar{x}$=mean of values of x
$\bar{y}$=mean of values of y
Sx^2, Sy^2, Sxy=sums of squares and products about the mean values $\bar{x}$, $\bar{y}$
b=regression coefficient of y on x
$s_{y.x}$=standard deviation from regression (standard error of estimate)
a=y intercept of regression line

In the course of fitting regression lines to the data of table 1, it was discovered that a few measurements were quite obviously in error. These were discarded in fitting the final regressions and in subsequent covariance studies. The snout to insertion of anal of the 1577-mm. specimen measured on November 12 was recorded as 970 mm. This point fell about 6 standard deviations away from the regression line computed from data including it. Since such an extreme deviation is unlikely, and since if the value of the ordinate were 870 mm. it would fall very near the regression line, it was regarded as most probably a recording error and was discarded from the computations. Similarly, the length of base of first dorsal of the 1114-mm. specimen measured on November 14 was recorded as 162 mm., a value almost 7 standard deviations away from the regression line computed from data including it. If the value were 262 mm. it would fall very near the regression line. This value was similarly presumed to have been a recording error and was therefore discarded in the final computations. The 807-mm. tuna measured on November 14 was recorded as having a second dorsal fin 196 mm. in length. This value is probably also a recording error, being over 4 standard deviations away from the regression line computed from the data with this point included, and was therefore discarded in the final computations.

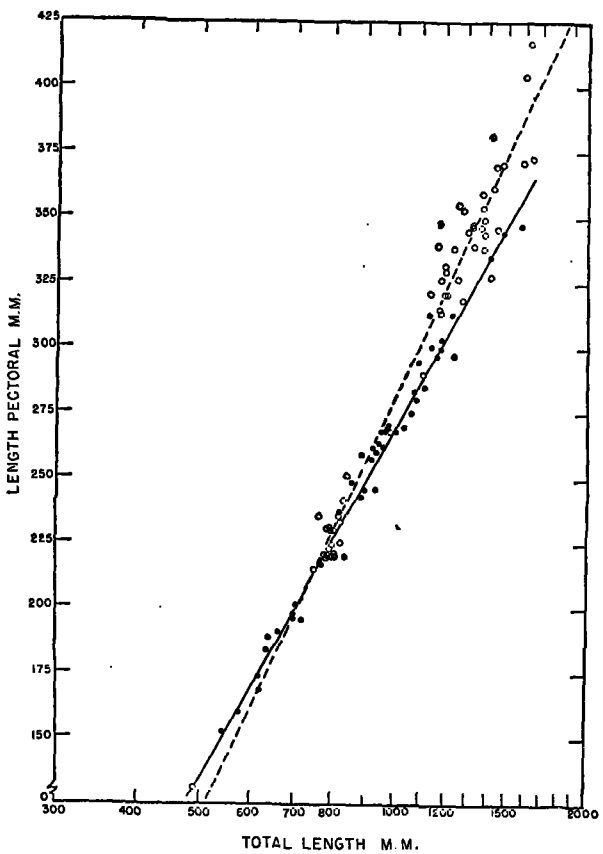

FIGURE 1.—Regressions of length of pectoral fin on logarithm of total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

The length of the second dorsal fin, 531 mm., of the 1468-mm. specimen measured on November 14 lies 3.5 standard deviations away from the regression line (fig. 2) of log of fin length on log of total length. This is a much greater deviation than one can reasonably expect to encounter among a series of 60 random samples from a homogeneous population. However, this same specimen had an anal fin 570 mm. long, which lies 2.8 standard deviations away from the line of regression of log of anal fin length on log of total length (fig. 3). This value is again a little larger than can reasonably be expected to be encountered in random sampling from a homogeneous population. These values of second dorsal fin length and anal fin length are such, also, that they fall very nearly on the line of regression of anal fin length on second dorsal fin length (fig. 4). It was concluded, therefore, that these fin lengths were correctly measured and recorded but that this particular fish had second dorsal and anal fins longer than might be expected from the values encountered among the remainder of the sample. Again, a specimen 1448 mm. long had an anal fin only 277 mm. in length, which is a good deal shorter than would be expected to occur by chance alone, being about 3 standard deviations away from the regression line. In this connection, however, it should be noted that the standard error of estimate employed here is the mean-square deviation about the regression line. As may be seen from a close inspection of figures 2 and 3, and as was pointed out by Schaefer (1948), the variability tends to increase with size of fish so that for large fish the actual range of variation which we may expect to encounter in random sampling will be somewhat greater than the value computed from the mean-square deviation from regression of all values in the sample. Considering this fact, these extreme deviations of fin

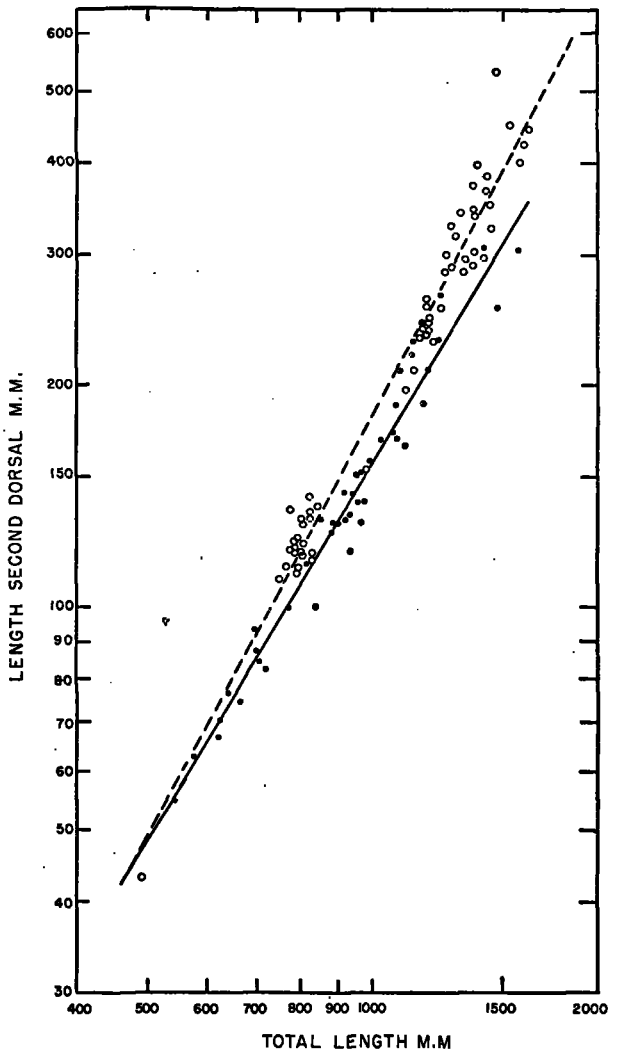

FIGURE 2.—Regressions of logarithm of length of second dorsal fin on logarithm of total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

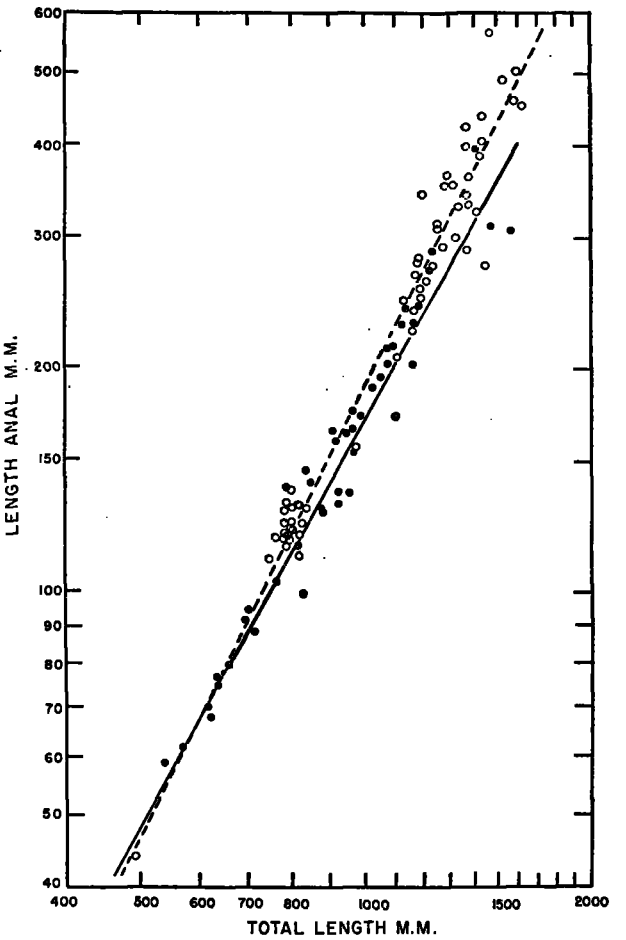

FIGURE 3.—Regressions of logarithm of length of anal fin on logarithm of total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

lengths may not be entirely improbable as having been drawn from the same population as the rest of our sample; they were therefore retained.

In the case of Costa Rican yellowfin tuna, Schaefer (1948) found that the relationship between length of pectoral and total length was nonlinear, but that plotting length of pectoral on logarithm of total length yielded a linear regression. For yellowfin tuna from Angola, the length of pectoral plotted against total length yields a regression much more nearly linear than is the case for the Costa Rican material. Indeed, a linear relationship between the original variables appeared to be a fairly good "fit" to the points. However, the employment of a linear regression of pectoral fin length on logarithm of total length, which for these data from Angola leads to the mean square regression

$$y=537 \log_{10} x-1{,}332$$

results in a very significant reduction of sum of squares of deviations from the regression line over the sum of squares of deviations obtained employing a linear regression between the original variables. It was concluded, therefore, that the growth law adduced for relative growth of pectoral fin length

and total length of Pacific yellowfin gave the best fit to the Atlantic data also. The data and the fitted regression line are shown in figure 1.

Growth of the second dorsal and anal fins relative to body length was found to be well fitted by the equation

$$y = cx^b$$

where y is fin length, x is total length, and c and b are constants, yielding a linear relationship when the logarithm of fin length is plotted against logarithm of total length (figs. 2 and 3). Where the measurements are in millimeters, the equations fitting our African yellowfin data are for second dorsal length on total length

$$y = .000378x^{1.895}$$

and for anal length on total length

$$y = .000179x^{2.008}$$

From these equations it may be seen that the length of second dorsal and anal fins are in proportion to the 1.90 power and the 2.01 power, respectively, of the total length. These values are sufficiently nearly equal that the regression of length of anal on length of second dorsal is well represented by a straight line (fig. 4).

COMPARISONS WITH PACIFIC TUNA

The comparison of body form of these specimens of *N. albacora* from waters off Angola with similar specimens of *N. macropterus* from waters off Central America, the measurements of which were recorded by Schaefer (1948), is of interest from two standpoints. First, there is the question whether the yellowfin tuna from the Atlantic and those from the Pacific are actually members of a single species or whether they belong in separate species. Second, regardless of whether they are to be placed in one or in two species, it is of interest to determine how much difference is found in body form among *Neothunnus* from widely separated regions of the world, mixing of fish between which is not likely, as a possible basis of judging the significance with respect to racial distinctness of fish from various parts of the same ocean. It seems unlikely that the yellowfin tuna from the Pacific Ocean off Central America intermix with yellowfin tuna from the Atlantic off Angola. Migration around the southern tip of Africa and across the Pacific is not entirely impossible, since during at least a part of the year the waters off the Cape of Good Hope are of high enough temperature to be inhabitated by these fish. Such a migration, however, seems sufficiently unlikely that we may assume that there is a high degree of likelihood that the yellowfin tuna from waters off Angola and the yellowfin tuna from the Pacific Ocean off Central America are separate and distinct populations. If the degree of morphological difference is a function of degree of separation of populations, the differences between these two populations may then indicate the kind and degree of differences to be expected between distinct and well-separated populations of yellowfin tuna.

Since, as we have pointed out earlier, body-proportion ratios or "biometric indices" vary with size of fish, their suitability for comparing measurements of fish from different populations is very limited. We have, therefore, employed the regressions of table 2 and similar regressions from Schaefer (1948) as a basis of comparison by means of the analysis of covariance. In our analyses we have followed the procedures set forth by Kendall (1946) page 237 *et seq.*

Perhaps the most striking difference exhibited by our samples between the Atlantic and Pacific yellowfin is in the length of the pectoral fin relative to the length of the body. As illustrated in figure 1, the same type of relationship fits the data from both samples, but the regression coefficients are markedly different. For both Atlantic and Pacific yellowfin tuna the length of pectoral fin relative to length of body decreases as the size of the fish increases, but the rate of decrease is more rapid for Pacific than for Atlantic fish. In consequence, among small sizes the length of pectoral is about the same for Atlantic and Pacific specimens, but among large fish the Atlantic yellowfin tuna have pectorals which are, on the average, very much longer than those of Pacific yellowfin tuna.

An equally marked difference between fish from the two places is observed in the relative growth of the second dorsal and anal fins (figs. 2 and 3). In both cases, the regression coefficients for the Atlantic yellowfin are very significantly [1] larger than for the

[1] In this paper a probability of one chance in a hundred is taken as the maximum value for a conclusion of significance, except where otherwise stated.

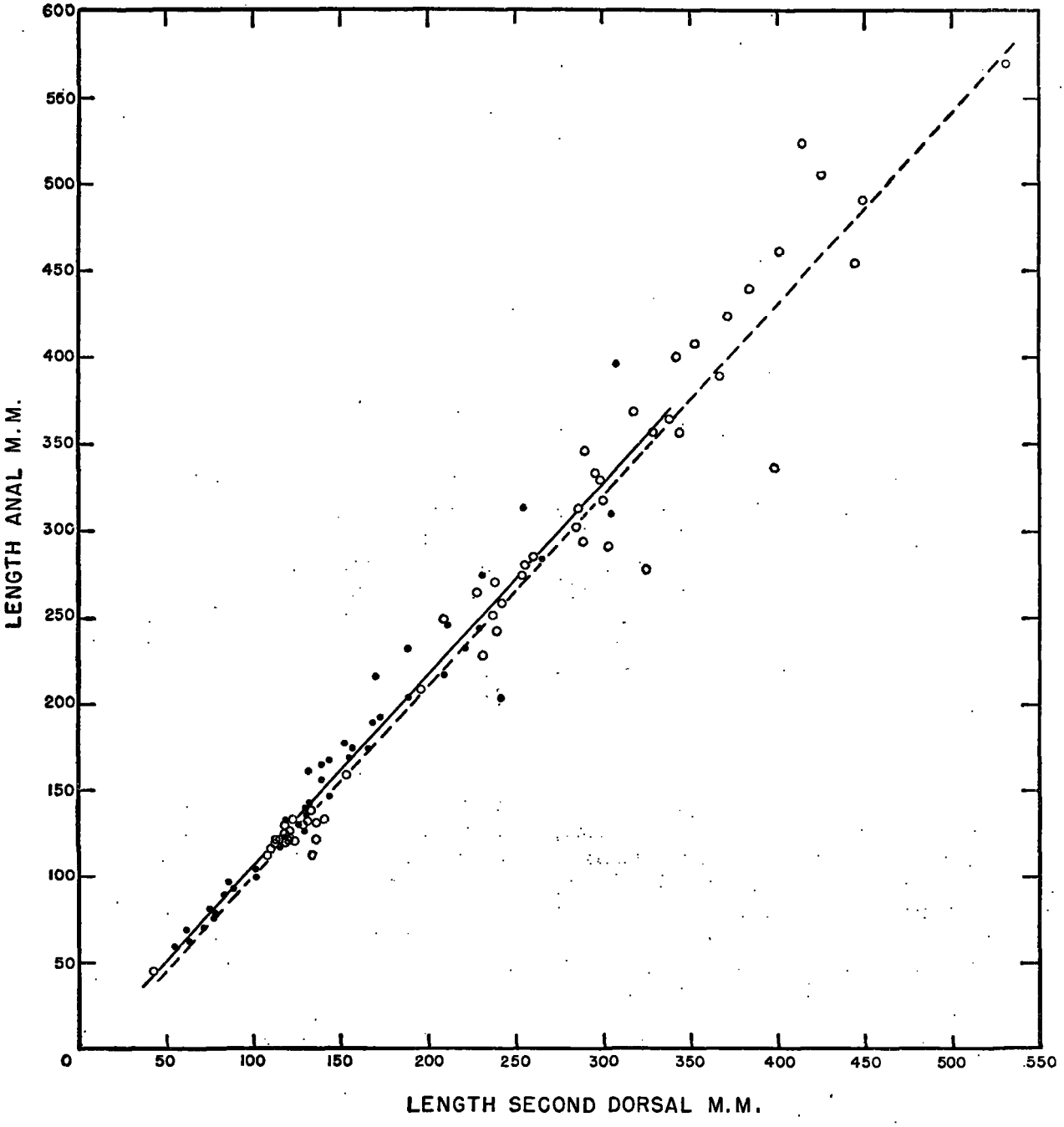

FIGURE 4.—Regressions of length of anal fin on length of second dorsal fin for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

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Pacific yellowfin. The second dorsal and anal fins of Pacific tunas grow much faster than the body, so that large fish have fins very much longer in proportion to body length than do small fish; in Atlantic yellowfin this phenomenon is even more marked. Among small fish there is little difference between specimens from the two localities, but larger fish from the Atlantic have fins very significantly longer on the average than those from the Pacific.

Although the second dorsal and anal fins of the Atlantic yellowfin tuna grow much more rapidly than those of the Pacific yellowfin tuna, the relation of length of anal to length of second dorsal is the same, on the average, for both groups (fig. 4); there is no significant difference between the regression equations.

The regressions of length of head, snout to insertion of first dorsal, snout to insertion of second dorsal, and snout to insertion of anal are in each case slightly but quite significantly different between the Atlantic and Pacific samples. In each case, as may be seen from figures 5 to 8, the regression coefficient for the Atlantic fish is smaller than the regression coefficient for Pacific fish. Furthermore, in each of these cases the regression lines cross one another in the neighborhood of a meter of total length. This consistency of results in each of these four cases argues even more strongly than the results of individual covariance analyses that there is a real difference in relative growth rates involved, if our samples are indeed representative of the populations from which they were drawn. There is indicated a small but definite difference in the growth of the head, and perhaps of the anterior part of the body, relative to total length, the rate of growth decreasing more rapidly for Atlantic than Pacific fish. Among small fish below about a meter in total length, the length of the head and the distance from the snout to the insertions of first dorsal, second dorsal, and anal fins is, on the average, slightly greater for Atlantic fish than for Pacific fish, while for larger fish above about a meter in total length these dimensions are, on the average, greater for Pacific fish than for Atlantic fish.

Covariance analysis of the data on what we term length of base of first dorsal, which is actually the distance from first dorsal insertion to second dorsal insertion, (fig. 9) indicates that the regression coefficients are sufficiently similar that the slight difference between them could very well have been the result of random sampling. However, there is a very significant difference between the levels of the two regression lines. It appears that over the range of sizes included in this study there is at each size of fish a small constant difference between the lengths of bases of first dorsals of Atlantic and of Pacific fish, the distance being shorter for Pacific tuna. This conclusion must, however, be approached with a good deal of caution because the data for this character for the Pacific fish have been shown to be peculiar in some inexplicable respect. It was noted by Schaefer (1948) that there was a significant difference between his measurements and those made by his coworker, J. C. Marr, with respect to the levels of the regression lines resulting from their sets of data treated separately. A comparison of our Atlantic measurements with the measurements by Schaefer alone, the regression line of which is closest to the regression line of the Atlantic tuna data, shows, however, that while there is no difference in regression coefficients there is a small but significant difference attributable to class means. It appears likely, therefore, that there is actually a small difference in this dimension between the two yellowfin-tuna populations in question.

The regressions of length of longest dorsal finlet on total length (fig. 10) are not to be regarded as different for the two groups of tunas since analysis of covariance shows that the probability of two such samples arising from a single homogeneous population is greater than one chance in twenty.

Although there is no significant difference between the two groups with respect to the length of longest dorsal finlet, it appears that there is a difference in the location of the longest finlet. Among the fish examined by Schaefer and Marr from the Pacific, the longest finlet was always No. 5 or No. 6 (enumerated from the most posterior forward). Among the yellowfin tuna examined from the Atlantic, however, No. 4 was the longest in 13 cases out of 16, as may be seen from table 1.

It is doubtful whether there exists a difference between the two populations in diameter of iris relative to head length. The regression coefficients are nearly identical for the two groups (fig. 11), but there might be a difference in the levels of the two lines. In testing the hypothesis that the two sets of data might have been drawn from the same population we arrived at a probability lying between 0.05 and 0.01, and a similar level of probability is arrived

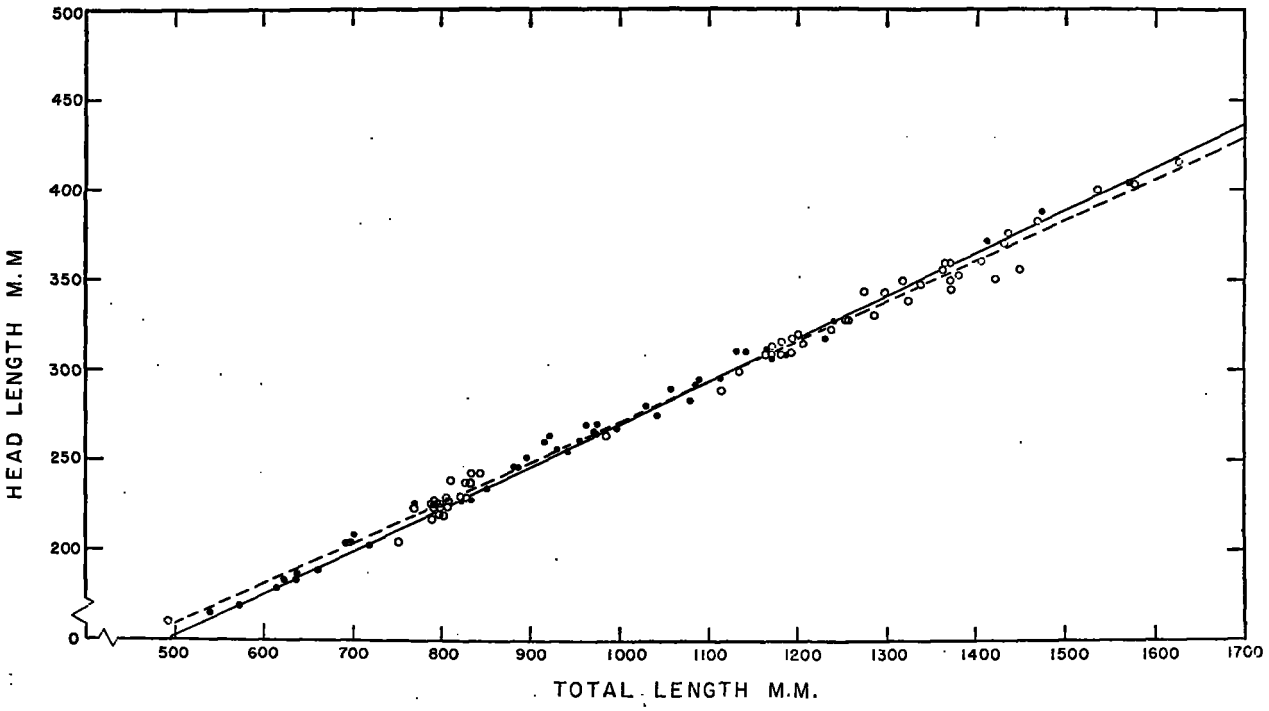

FIGURE 5.—Regressions of head length on total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

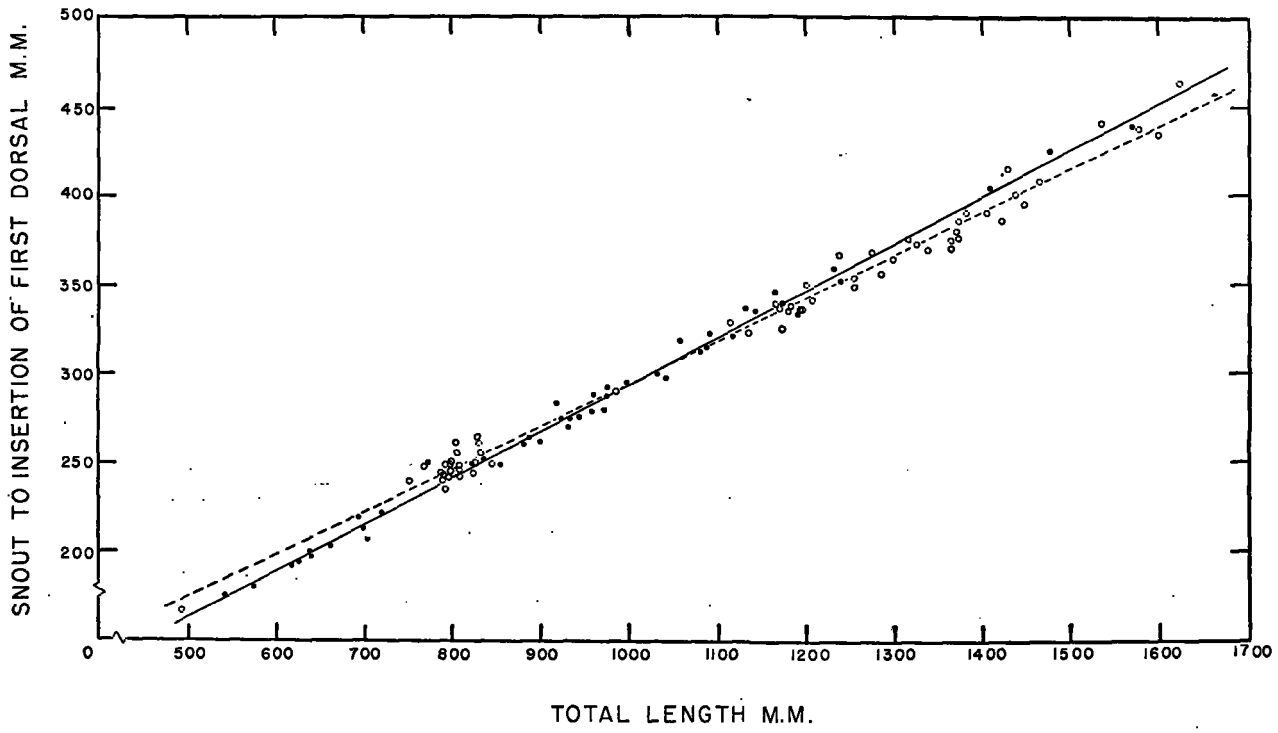

FIGURE 6.—Regressions of distance from tip of snout to insertion of first dorsal fin on total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

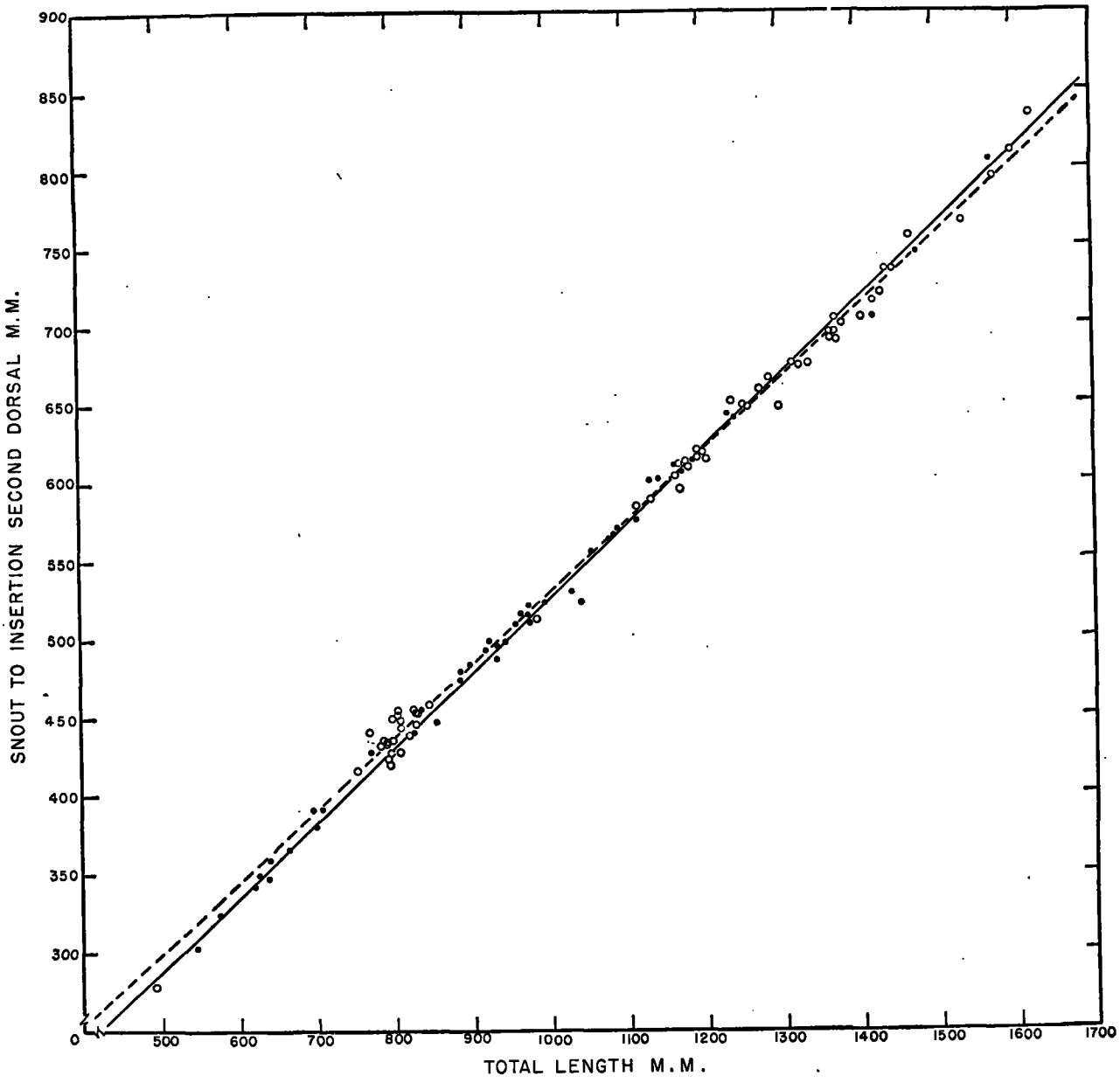

FIGURE 7.—Regressions of distance from tip of snout to insertion of second dorsal fin on total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

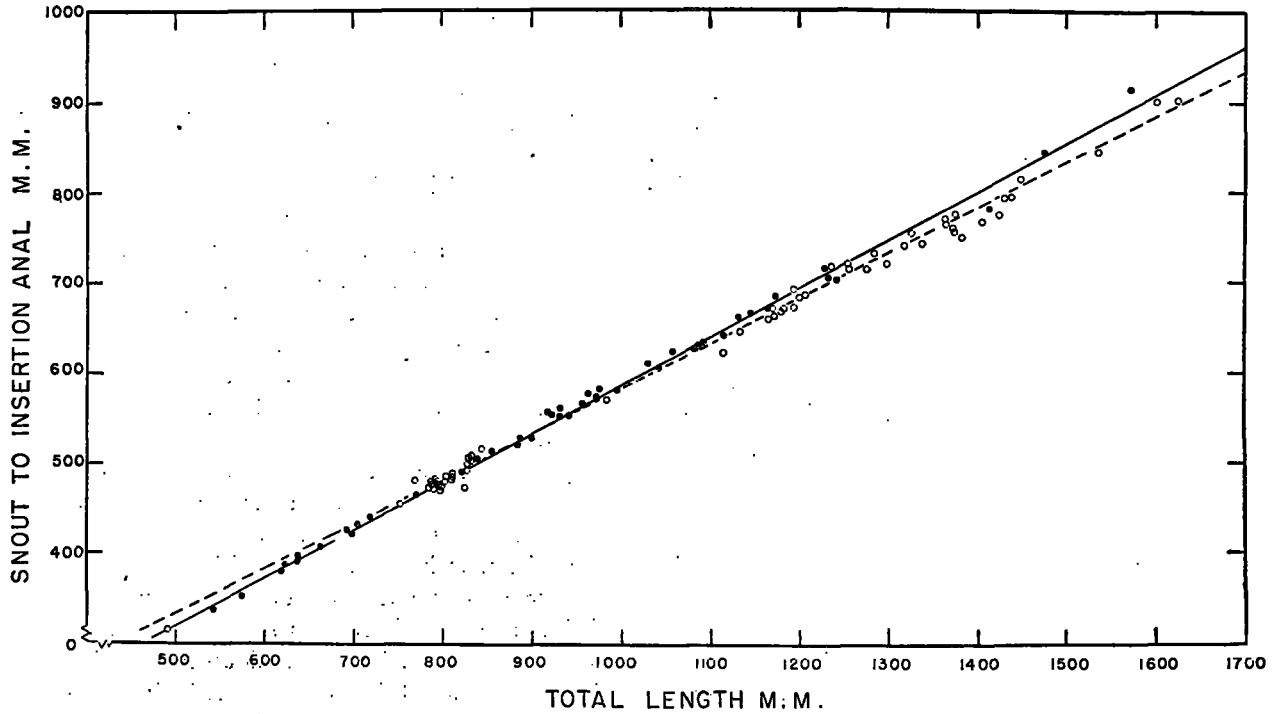

FIGURE 8.—Regressions of distance from tip of snout to insertion of anal fin on total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

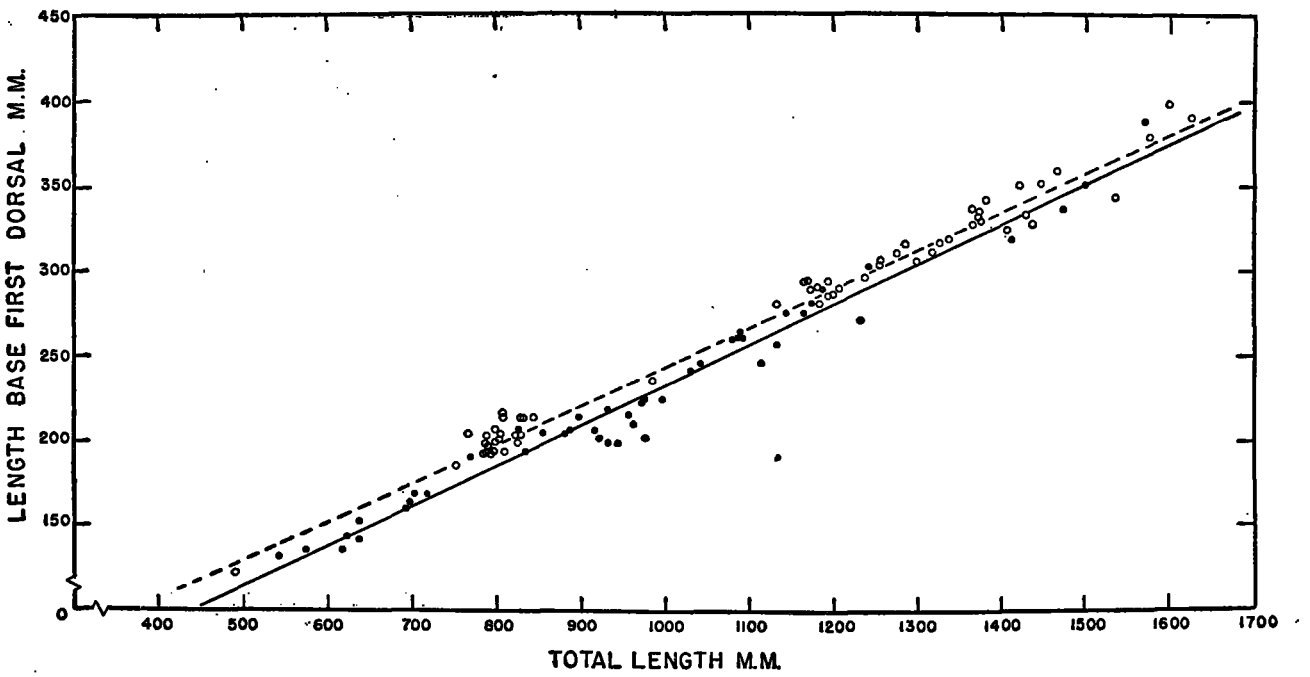

FIGURE 9.—Regressions of length of base of first dorsal on total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

at when the variance due to difference between class means is compared with the average variance within classes. The difference in the levels of the two lines in figure 11 cannot, therefore, be concluded to be significant, although the probability values are such that the possibility of the existence of such a difference between the populations cannot be ruled out either.

Covariance analyses indicate that our data show no significant differences between the Atlantic and Pacific samples with respect to the regressions of length of maxillary on head length (fig. 12), greatest body depth on total length (fig. 13), pectoral insertion to insertion first dorsal on total length (fig. 14), or length of longest dorsal spine on total length (fig. 15).

The gill-raker counts of these 19 Atlantic yellowfin have a mean value of 30.00, while among 45 Pacific yellowfin studied by Schaefer (1948) the mean value was 30.60. The difference between these means, considered with the associated variances, yields a value of "t" of 1.79, which would occur by chance in between 5 percent and 10 percent of random samples from a single population with normally distributed counts. These data reveal, then, no significant difference in mean gill-raker counts.

There appears to be some difference in finlet counts between the Atlantic tunas and the Pacific specimens with which we are comparing them. As may be seen from table 1, a total dorsal finlet count of 9 characterized each of the 19 Atlantic yellowfin tuna on which counts were made. Schaefer's table 1 shows that of the 46 counts made by him and Marr, a count of 10 was recorded in 42 cases, with a count of 9 in only two cases, one case being questionable and one fish having 9 finlets but being an abnormal specimen with the sixth finlet obviously missing. It appears that the Atlantic yellowfin tunas have usually one less dorsal finlet than their Pacific counterparts.

Similarly for Atlantic yellowfin there were counted 9 anal finlets in 18 cases and 7 in 1 case, while for Pacific yellowfin the counts of anal finlets were as follows: 10 finlets in 20 counts; doubtful whether 10 or 9 in 4 counts; 9 in 17 counts; doubtful whether 9 or 8 in 4 counts; and 8 in 1 count. Assigning the doubtful counts to the lower value in each case, this yields

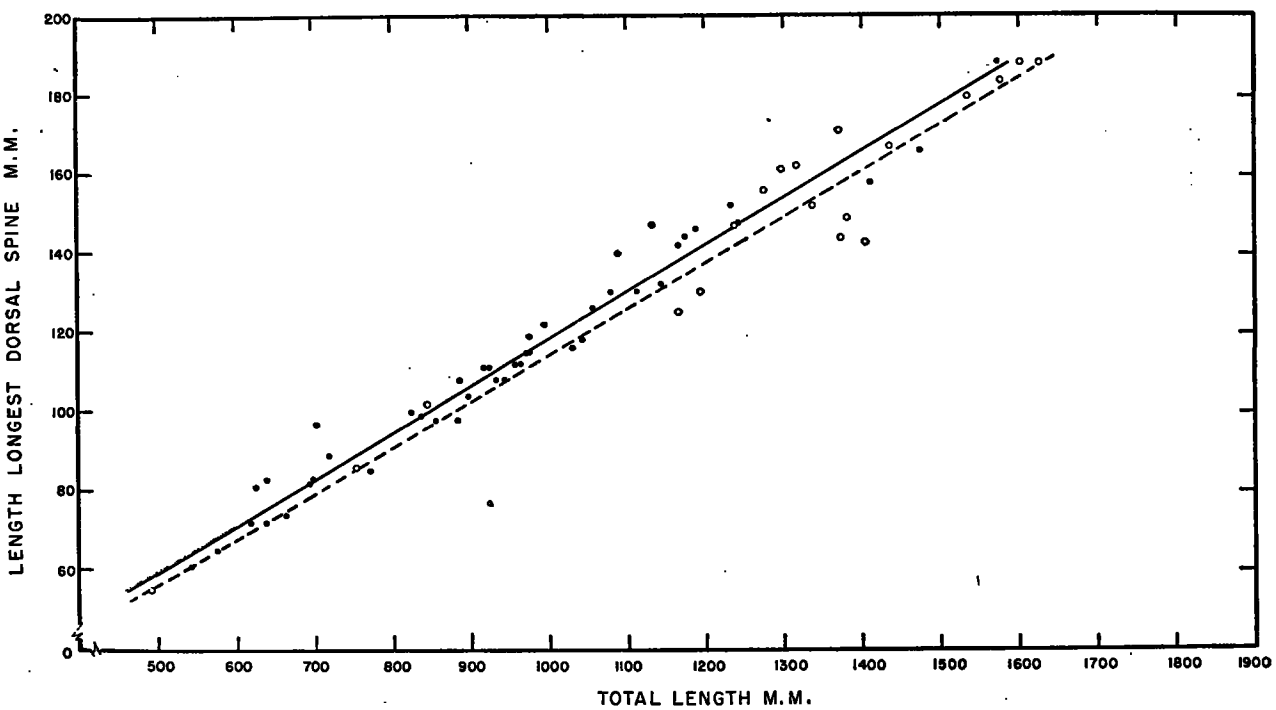

FIGURE 10.—Regressions of length of longest dorsal finlet on total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

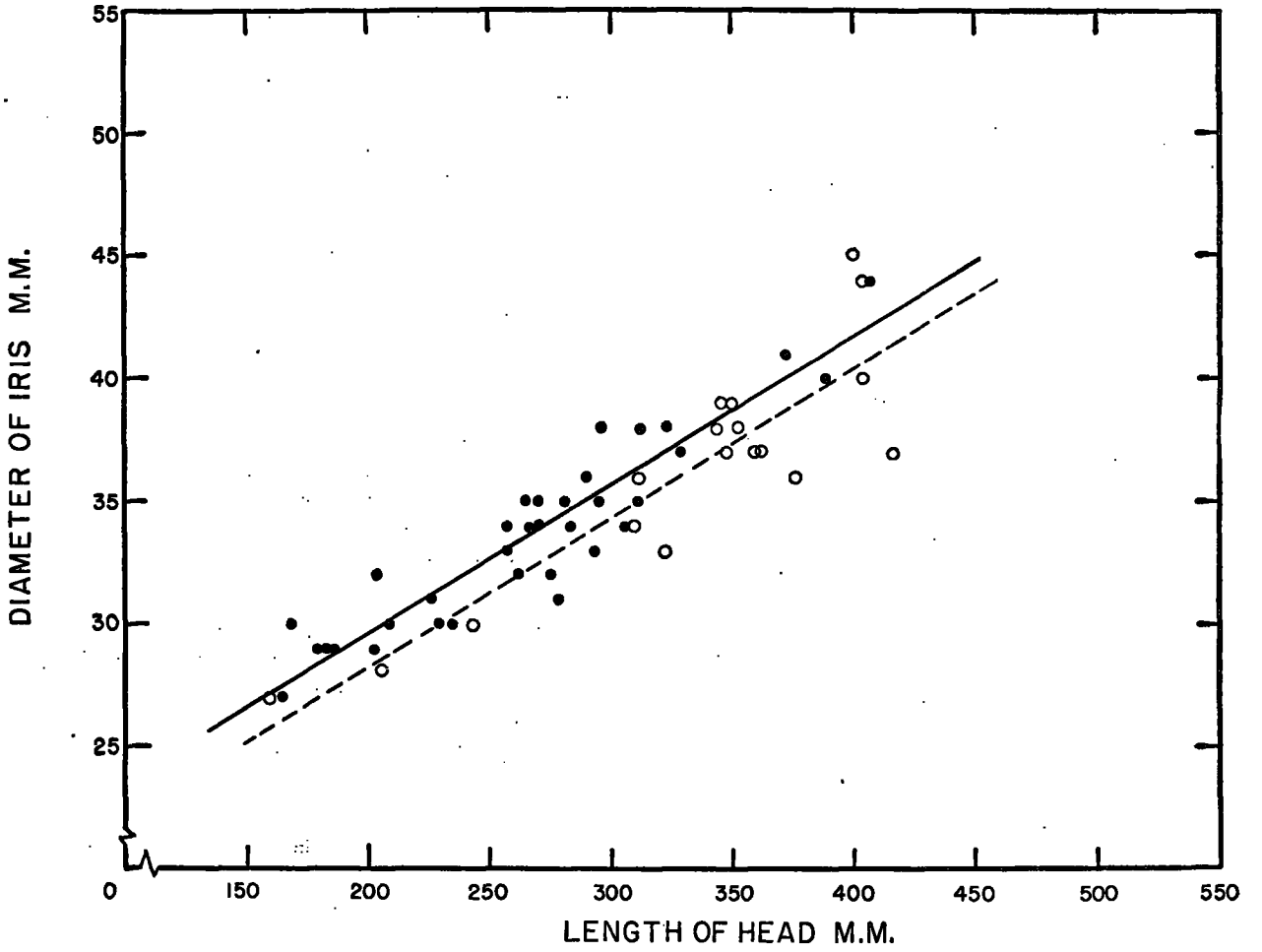

FIGURE 11.—Regressions of diameter of iris on length of head for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

a mean anal-finlet count of 9.33 for the Pacific specimens compared with 8.89 for the Atlantic. The difference between these means, 0.44, is associated with a probability, judged from the "t" distribution, just greater than one chance in a hundred and hence, probably significant. In view, however, of the difficulty of deciding between an attached finlet and the posterior ray of the anal fin, we hesitate to assert with certainty that the finlet counts are actually different for the two populations of tuna under consideration, the observed difference being possibly due to differences between observers rather than differences between the specimens observed.

COMPARISONS WITH DATA IN LITERATURE

Frade (1929) measured a series of 50 specimens from the Canary Islands and from the measurements computed various body-proportion ratios, which he calls "indices biométriques." For each such index he published the mean value and the extreme limits encountered among his data. The sizes of the fish measured are not given. In 1931 he published similar mean indices and observed limits for a sample of 100 fish from the Canaries, ranging in size from 99 cm. to 174 cm.

Four of Frade's indices are composed of dimensions that are nearly equivalent to dimensions measured by us. These are recapitulated in our table 3, together with the corresponding indices, computed from the regressions of our table 2, for the fish of mean length in our sample. We also give the "expected limits" of the index within the range of total lengths 990 mm. to 1740 mm. These "expected limits" are the ratios obtained by employing the y values of the regression equation corresponding to the x values 990 or 1740 mm. plus or minus 2.576 standard errors of estimate. For example, the regression of head length on total length (fig. 5) indicates that for the mean fish, which is 1114 mm. long, the head length is 297 mm., yielding a ratio of 3.75. At a total length of 990 mm. the average head length is 268 mm.; adding 2.576 standard errors of estimate (14.8), we obtain 282.8 giving a ratio of 3.50 as the minimum value expected. Similarly, at a total length of 1740 mm. the average head length is 439 mm.; subtracting 2.576 standard errors of estimate (14.8), we obtain 424.2 mm., yielding a ratio of 4.12 as the maximum expected value. The value 2.576 in these computations is the value of "t" corresponding to a probability level of one chance in a hundred. Thus, the expected limits in our table 3 are the values that would be expected to be exceeded less than one time in a hundred among any sample drawn from this size range, regardless of its size composition.

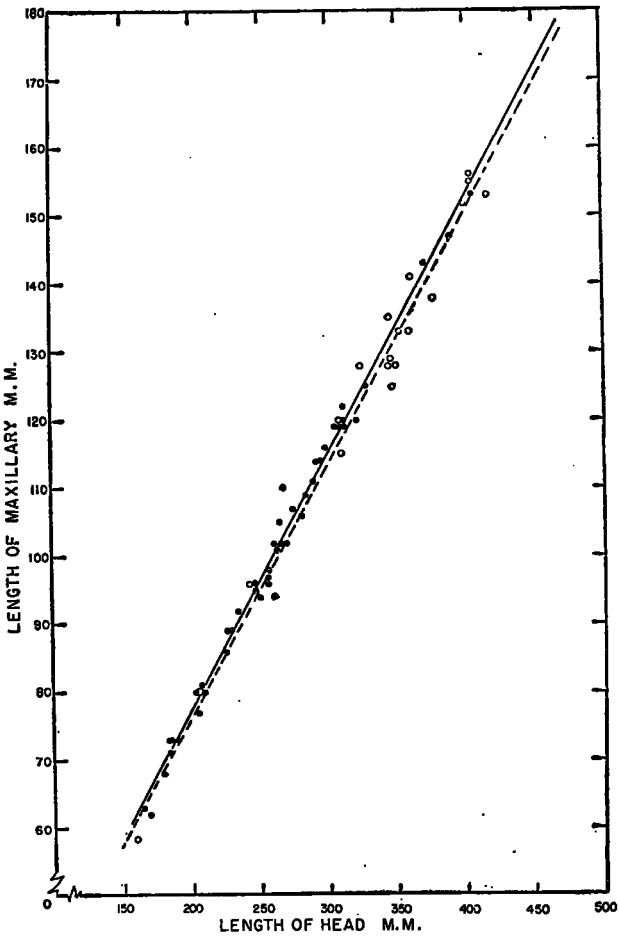

FIGURE 12.—Regressions of length of maxillary on length of head for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

Since our largest fish was 1626 mm. in total length, the computation of values corresponding to a total length of 1740 mm. represents a slight extrapolation of the regressions calculated from our data.

It may be seen from table 3 that the ranges of values of body-proportion indices encountered by Frade among yellowfin tunas from the Canary Islands are similar to those computed from our Angolan data. So far as these data go, the fish from the two localities may not be concluded to be morphometrically different. However, in view of the large ranges of values resulting from differential growth rates, as discussed previously, it would not be expected that any except very large differences would be detected by such indices. These data may illustrate the lack of precision of the statistics employed rather than the similarity of the morphology of the fish involved.

Frade also gives finlet counts for the specimens reported on in both 1929 and 1931. Nine finlets for both dorsal and anal series were most common. For his 1931 counts he reports a mean value of 9.06 with a probable error (.6745 standard errors) of 0.266 for the dorsal finlet counts and a mean value of 8.98 with a probable error of 0.285 for the ventral finlet counts. These values are not significantly different from the counts recorded for our Angolan specimens, but are very close to our mean values of 9.00 for dorsal finlets and 8.89 for anal finlets.

The lengths of second dorsal, anal, and pectoral fins of the one specimen, of 170 cm. from snout to fork of caudal, for which Frade (1929) gives the original measurements fall sufficiently close to the respective regression lines of our Angolan data to be well within the probable limits of random variation. At the

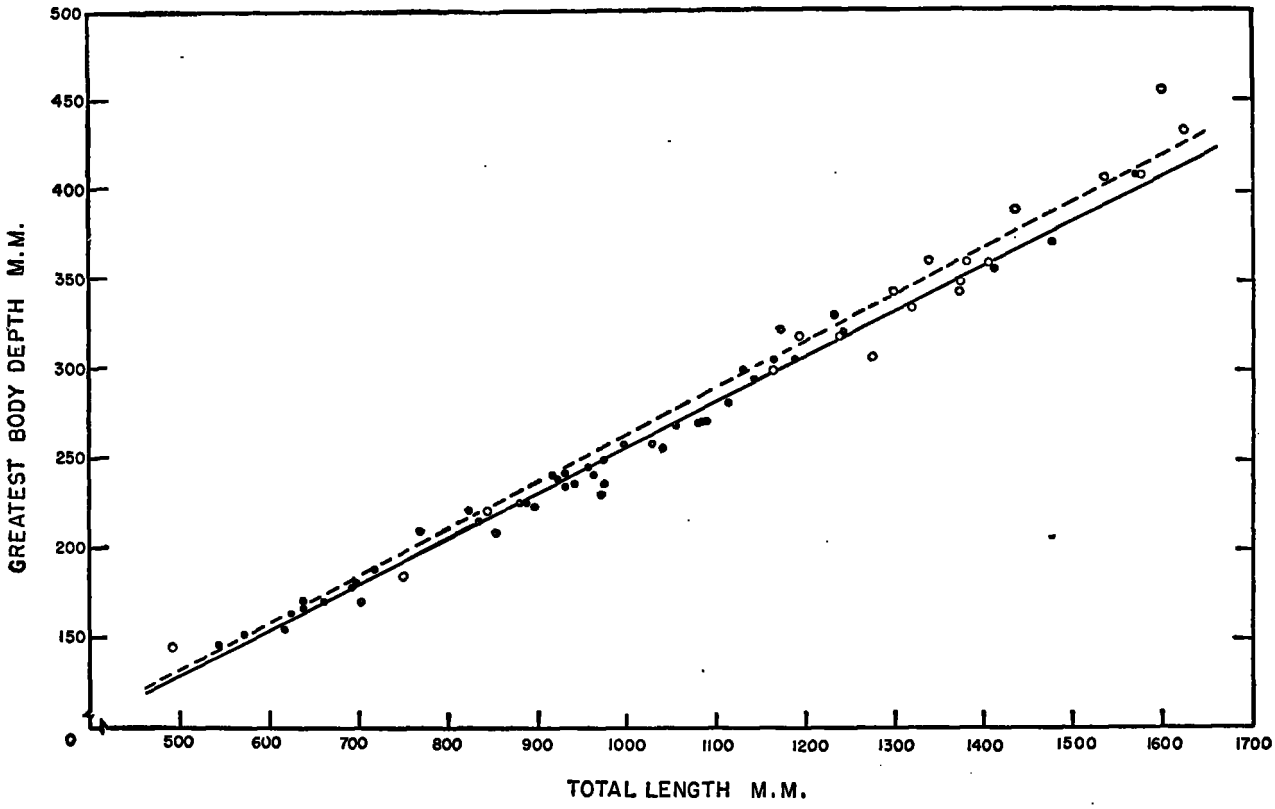

FIGURE 13.—Regressions of greatest body depth on total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

TABLE 3.—*Comparison of body proportion ratios of yellowfin tuna recorded by Frade from the Canary Islands with similar data from Angola*

Ratio	Frade's Index	Frade, 1929		Frade, 1931		Angolan regressions	
		Mean	Limits observed	Mean	Limits observed	Mean fish	Expected limits in range of total lengths 900 mm. to 1740 mm.
$\frac{\text{Total length}}{\text{Length of head}}$	Ti	3.83	3.57–4.07	3.86	3.50–4.20	3.75	3.50–4.12
$\frac{\text{Total length}}{\text{Length of pectoral}}$	Pi	4.03	3.57–4.72	4.08	3.45–4.65	3.62	3.19–4.60
$\frac{\text{Total length}}{\text{Snout to insertion first dorsal}}$	Di	3.54	3.15–3.95	3.52	3.10–4.00	3.45	3.18–3.82
$\frac{\text{Total length}}{\text{Snout to insertion second dorsal}}$	Dii	1.76	1.81–2.07	1.94	1.70–2.10	1.92	1.81–2.03

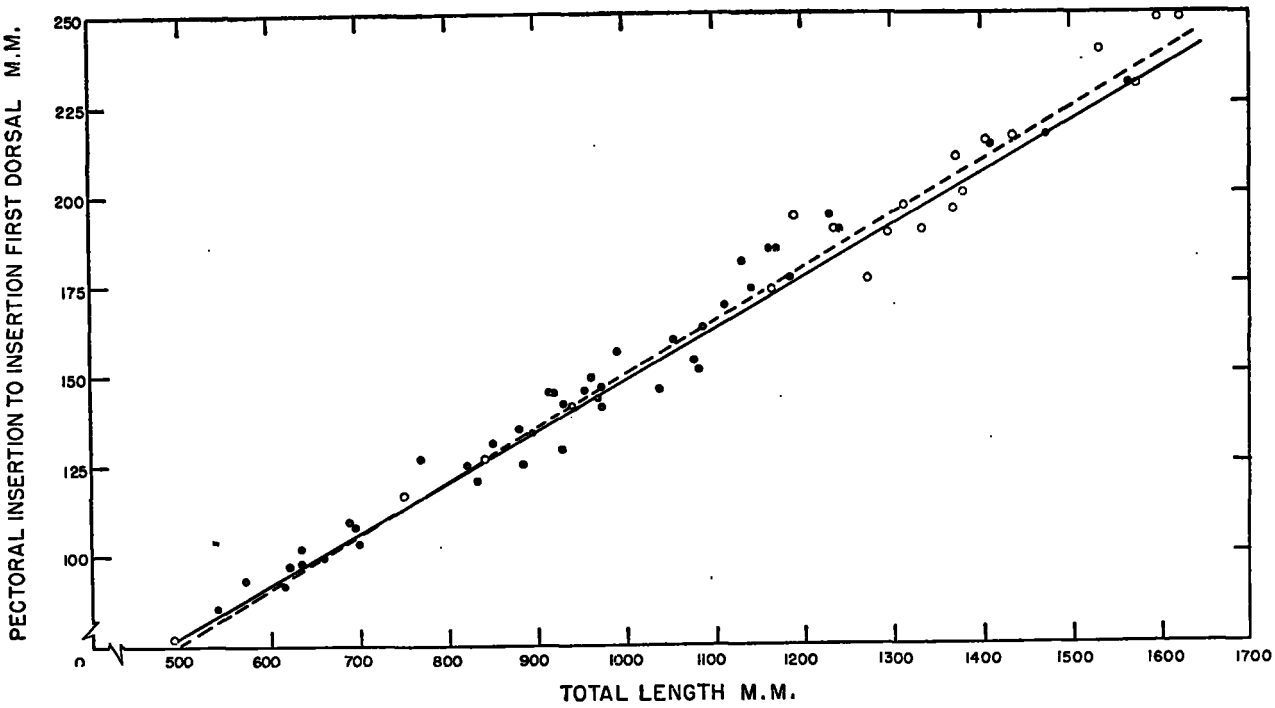

FIGURE 14.—Regressions of distance from insertion of pectoral fin to insertion of first dorsal fin on total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

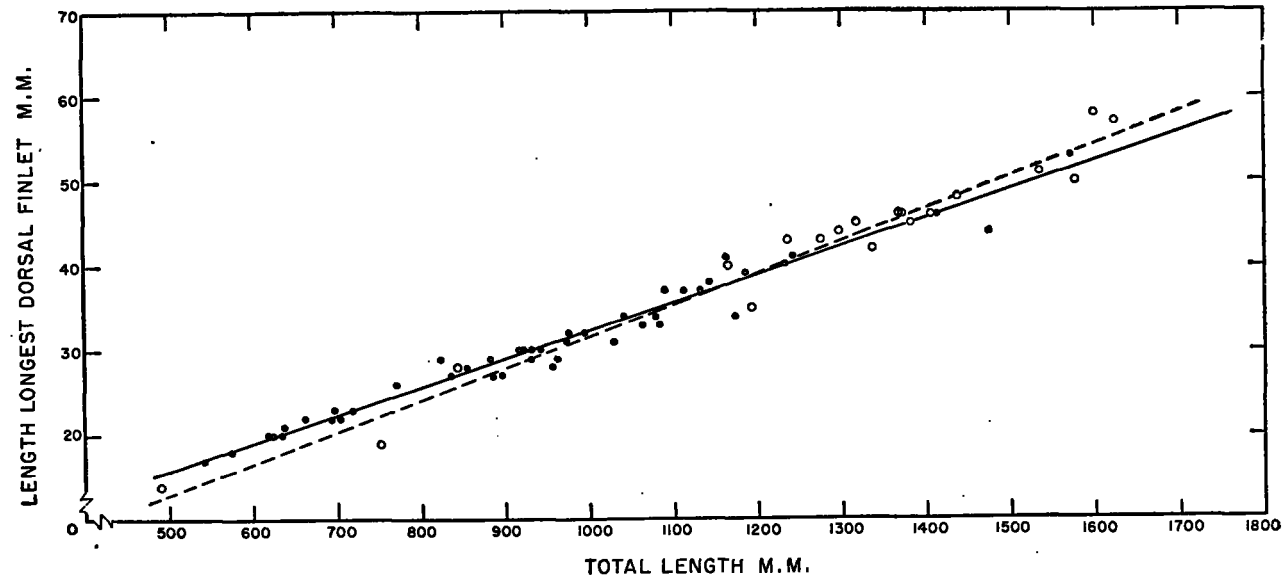

FIGURE 15.—Regressions of length of longest dorsal spine on total length for yellowfin tuna from the Atlantic Ocean off Angola (open circles and broken line) and for yellowfin tuna from the Pacific Ocean off Central America (solid circles and solid line).

same time the lengths both of the second dorsal and anal fins are sufficiently great to fall outside the values that would be expected to occur by chance deviation in one case in a hundred from the regression lines fitting the Pacific data studied by Schaefer (1948).

So far as these data go, the Canary Islands yellowfin appear to be similar to our Angolan yellowfin.

Nichols and LaMonte (1941) refer to a Portuguese specimen "about 5 feet" long having soft dorsal and anal fins contained "2.6 to 2.8 times in the length." For both fins this falls well within the expected limits of variation of our Atlantic material at this size.

From the western side of the Atlantic, Beebe and Tee-Van (1936) give on page 189 the lengths of second dorsal and anal fins of fish from the Carribean area in percent of standard length, together with the standard lengths of the specimens in question. Since their fish are recorded according to standard length, exact comparisons with our data are difficult. From their measurements of the 577 mm. specimen on page 191 it appears that at this size there is a difference of 22 mm. (4 percent) between the standard and total lengths. From Frade's data on a fish of 1700 mm. total length it appears that the correction factor at this size is about 9 percent. With or without the application of a correction factor for the difference between standard and total length, Beebe and Tee-Van's three smallest specimens (555, 645, and 690 mm. standard length) fall well within the limits of fin lengths expected from the regression lines and associated variances for our Angolan yellowfin. The 930-mm. specimen has a second dorsal fin a bit shorter than one would expect, but little weight can be given to this because the measurements were made from a photograph and are probably not very accurate. The 1220-mm. specimen also has second dorsal and anal fins falling within the expected range of our Angolan material, whether or not a 9-percent correction is added to the length as recorded by Beebe and Tee-Van. For the 1360- and 1450-mm. specimens, however, the converse is the case for length of anal fin. With or without a correction for standard length, both of these specimens have anal fins falling well outside the expected limits of variation of our Angolan material, even considering the fact that the variability increases with size of fish. The second dorsal fins of these two fish fall near the extreme upper limit of the expected variation about the regression line if a correction of 9 percent is added to the length recorded, and fall well outside the limit if such a correction is not applied. It appears that these specimens certainly had anal fins longer than would be expected on the basis of our Angolan sample and probably had second dorsals that were outside the expected range.

Nichols and LaMonte referring to "Allison's tuna" from St. Lucia state: "At about 4 feet 5 to 9 inches . . . the lobes are contained 2.1 to 2.8 times in standard length." These fin lengths are quite significantly longer than we would expect on the basis of our Angolan regressions and observed variances about them.

DISCUSSION

Beebe and Tee-Van (1936) synonymize *Thynnus albacora* (Lowe) 1839 with *Thynnus argentivittatus* (Cuvier and Valenciennes) 1831. Nichols and Murphy (1922) identified a photograph of a specimen from Peru as *argentivittatus*, and state that it agrees with Cuvier and Valenciennes' description and with a specimen in the Paris Museum labelled Malabar, Dussumier. On this basis Nichols and LaMonte (1941) disagree with Beebe and Tee-Van's use of *argentivittatus* for the Atlantic form, which they refer to *albacora*.

Examination of the description by Cuvier and Valenciennes reveals that they mention both a drawing by Quoy and Gaimard from the Atlantic and specimens collected from the Indian Ocean by Dussumier. We requested Dr. Leon Bertin of the Paris Museum to examine the material deposited there in order to determine which specimen should be designated the type of *argentivittatus*. He has kindly supplied the information that the specimens upon which Cuvier and Valenciennes' description of *Thynnus argentivittatus* is based are three in number:

One specimen from the Atlantic, a drawing by Quoy and Gaimard. Collection of the Paris Museum No. A5572.

One specimen from the Indian Ocean sent by Dussumier, preserved dry. Collection of the Paris Museum No. A5567.

One specimen from the Indian Ocean, Coast of Malabar, sent by Dussumier. This specimen, Paris Museum No. A5816, is preserved in alcohol. According to Dr. Bertin, it corresponds to the description and numerical data given by Cuvier and Valenciennes and should be considered as the lectotype. It is hereby so designated.

It appears that the Indian Ocean yellowfin tuna should be called *Neothunnus argentivittatus* (Cuvier and Valenciennes) 1831, that from the Atlantic *Neothunnus albacora* (Lowe) 1839, and that from the Pacific *Neothunnus macropterus* (Temminck and Schlegel) 1842, until such time as it is determined whether or not the Indian Ocean form is identical with one of the other two, in which case *argentivittatus* would displace *albacora* or *macropterus*. There is the further question, of course, whether the Atlantic and Pacific forms should not be considered subspecies or varieties of a single species of cosmopolitan distribution. As noted below, we feel this question cannot be answered satisfactorily until more information is available regarding variability within oceans compared with variability between oceans.

The morphometric data presented in the foregoing study indicate that there are marked differences in relative growth rates of certain fins and body dimensions of yellowfin tuna from the Pacific off Central America and from the Atlantic off Angola. There seem also to be differences in average number of finlets and in the position of the longest dorsal finlet. There appears to be ample evidence that these two tuna populations are separate and distinct groups of fish which, at large sizes at least, can be distinguished readily by morphological characters. Whether the degree of difference is sufficient to warrant placing them in separate species, or whether they should be classed merely as subspecies or races of the same species will depend, however, upon further studies of the degree of variation encountered among populations within each ocean. Pending completion of such studies we place them in separate species, *Neothunnus albacora* (Lowe) 1839 for the Atlantic form and *N. macropterus* (Temminck and Schlegel) 1842 for the Pacific form.

Examination of published data on yellowfin tuna from other parts of the eastern Atlantic Ocean indicates that they are similar to our Angolan samples, and in some respects are dissimilar to the Pacific yellowfin tuna. The data, however, are not sufficiently complete or published in a satisfactory form for critical statistical comparisons. It is highly desirable that comparable measurements be made of representative series from other parts of the eastern Atlantic, and that either the original measurements or the regression statistics, or preferably both, be made available for comparison with our material.

Similarly, the few data available in the literature indicate that large yellowfin tuna from the western Atlantic may differ from those of the eastern Atlantic. The lengths of the second dorsal and anal fins of large specimens from the West Indies seem to be appreciably longer than would be expected on the basis of our Angolan material. Again, it is to be desired that representative series covering the entire range of sizes available be measured from various western-Atlantic localities, and that the data be made available in suitable form for critical statistical comparison with similar data from other parts of the world.

Schaefer (1948) found that the anal and second dorsal fins of the yellowfin tuna from the Pacific off Costa Rica grow much faster than the body of the fish, so that large individuals have fins relatively much longer than have small individuals. He found that the second dorsal and anal fin lengths are in proportion to the 1.69 and 1.83 powers, respectively, of the total length of the fish. Similarly, our data indicate that the Angolan yellowfin tuna possess second dorsal and anal fins with lengths in proportion to the 1.90 and 2.01 powers, respectively, of the total length, so that here also the large fish have enormously longer fins than do small fish (figs. 2 and 3). There is very great variability, however, in the lengths of these fins among fish of the same size. The standard deviations about the regression lines, converted from the logarithms in table 2, amount to 9.6 percent for the second dorsal fin and 11.4 percent for the anal fin, values similar to but slightly larger than those reported by Schaefer from Costa Rica. These values of standard deviation represent the average of the squared deviations from the regression lines. As may be seen from figures 2 and 3, however, the variability is not entirely evenly distributed, the variation at large sizes being greater than at small sizes even on a logarithmic scale. Because of the great range in fin length, particularly among large fish, it has been noted by various authors writing on *Neothunnus* that there exist at the same total length specimens with long fins and other specimens with short fins. Some authors have placed the long-finned and short-finned specimens in separate species or varieties (Jordan and Evermann 1926, Frade 1931, Nichols and LaMonte 1941), but where extensive series have been examined it has usually been concluded that the short-finned and long-finned varieties

are merely extreme deviates of the same single population for a given locality (Herre 1936, Walford 1937, Schaefer 1948). Our data from Angola tend to confirm this view, although the occurrence, as described, of a single specimen with anal and second dorsal fins rather longer than might be expected to occur by chance from a single homogeneous population makes desirable further study of the matter, particularly in the western-Atlantic region where individuals with exceptionally long fins are reported to occur (Beebe and Tee-Van 1936) and from whence Allison's tuna (Mowbray 1920) was described.

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UNITED STATES DEPARTMENT OF THE INTERIOR, OSCAR L. CHAPMAN, *Secretary*
FISH AND WILDLIFE SERVICE, ALBERT M. DAY, *Director*

LARVAE OF TUNA AND TUNA-LIKE FISHES FROM PHILIPPINE WATERS

By CHARLES B. WADE, Aquatic Biologist
Illustrations by PABLO BRAVO

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LARVAE OF TUNA AND TUNA-LIKE FISHES FROM PHILIPPINE WATERS

By CHARLES B. WADE, *Aquatic Biologist*

This is the fourth in a series of papers concerned with the biology and taxonomy of the more common tuna and tuna-like fishes inhabiting Philippine waters. The data for this paper were collected from October 1947 through November 1949 by the biological staff of the Philippine Fishery Program[1] of the Fish and Wildlife Service aboard the oceanographic research vessel *Spencer F. Baird.*

Within an area of 810,000 square miles, and including both the Philippine and closely adjacent seas, 463 tows for larval fish and plankton were made as part of the routine biological operations. Collections were accumulated from off the Island of Celebes (Netherlands East Indies) in the south, to Taiwan (Formosa) in the north, and between 117° and 130° east longitude.

All tows except one (B-37)—a deep oblique haul—were made at the surface. In general the length of each tow was half an hour, although a few 1-hour tows were made (table 1). A standard meter net was used, and the materials collected were preserved in 4-percent formalin solution and returned to the shore laboratory in Manila for sorting and study. There the larval tuna and tuna-like fishes were separated from the mass of zooplankton, and this paper is based on the collection of larval forms.

Despite the abundance of the material collected, 1,842 specimens, the specific identification of many of the specimens could not be made accurately. A great number of specimens were less than 6 millimeters in length, and few characters were sufficiently developed to be used as criteria for identification. Large larval forms of 10 to 15 mm. in length are still unknown for many species, and until these can be collected and identified, accurate segregation of the smaller specimens is not possible.

The monotonous task of sorting the collections was performed capably by Godofredo Mijaro, laboratory technician. Dr. Hilary J. Deason, Chief, Office of Foreign Activities, Fish and Wildlife Service, advised on the preparation of the final text.

LARVAL-FISH AND PLANKTON TOWS

Tows for larval fish and plankton were made during 18 of the 29 months, or 62 percent of the time the *Spencer F. Baird* was stationed in Philippine waters. A station list is given in table 1. Field work began in October 1947, and 36 tows were made during the remainder of that year. Fifty-five percent, or 20 of these tows, produced 219 larval tuna-like fishes. The average number of tuna-like larvae collected per tow during 1947 was 6.1 specimens. Operations were carried on for 7 months during 1948. There were 152 tows during the year of which 50 tows (32.8 percent) produced 251 tuna-like larvae. The average catch for all tows in 1948 was 1.65 larvae. During 9 months of 1949, 112 tows (40.8 percent of the 275 tows) produced 1,372 larval tuna-like fishes. The 1949 average catch for all tows was 4.99 fish. During the entire period of field work, 463 larval fish and plankton tows were made, and 192 (41.5 percent) of these produced larval tuna-like fishes. A total of 1,842 larvae were collected, an average of 3.97 fish per tow for all operations. The monthly catches are shown in table 2.

[1] Part of the Philippine Rehabilitation Program authorized by the Philippine Rehabilitation Act of 1946, title 50, App. U. S. Code, sec. 1789.

TABLE 1.—*Station list of larval-fish and plankton tows made in Philippine waters, 1947–49, and number of tuna-like larvae found at each station*

Station	Date	Latitude	Longitude	Time of tow	Number of specimens
	1947				
B-5	17 Sept.	13°57′ N.	119°30′ E.	----------	----------
B-15	7 Oct.	11°45′ N.	121°24′ E.	0905–1005	----------
B-16	do	11°07.5′ N.	121°56′ E.	1605–1705	2
B-17	do	10°13′ N.	121°20′ E.	0100–0200	9
B-18	8 Oct.	10°08′ N.	122°09′ E.	0910–1000	----------
B-20	do	9°38.5′ N.	121°56.5′ E.	1540–1640	----------
B-21	do	9°02.5′ N.	122°31′ E.	2300–2400	----------
B-22	9 Oct.	8°41′ N.	122°50′ E.	0640–0740	1
B-23	do	8°20′ N.	122°47′ E.	1140–1240	----------
B-24	do	8°14′ N.	122°07.5′ E.	1550–1620	----------
B-25	10 Oct.	7°27′ N.	121°43′ E.	0109–0134	----------
B-26	do	7°04′ N.	121°35′ E.	2002–2032	----------
B-27	11 Oct.	7°45′ N.	121°45′ E.	0237–0252	----------
B-28	do	8°20′ N.	120°50.5′ E.	1122–1137	----------
B-29	12 Oct.	6°57′ N.	120°15′ E.	0457–0527	4
B-31	13 Oct.	9°31′ N.	119°40′ E.	(1)	
B-32	do	9°49′ N.	119°22.5′ E.	0455–0525	2
B-33	do	10°19′ N.	120°03′ E.	1145–1215	----------
B-34	do	10°02′ N.	120°21.8′ E.	1605–1705	5
B-35	do	9°44′ N.	120°38′ E.	2150–2250	16
B-36	14 Oct.	9°08′ N.	121°12.5′ E.	0541–0641	1
B-37	do	8°32′ N.	121°48.5′ E.	1625–1900	1
B-47	3 Dec.	9°03′ N.	118°58′ E.	1851–1951	9
B-48	4 Dec.	8°27.5′ N.	119°34′ E.	0230–0330	----------
B-49	do	7°51.5′ N.	120°10′ E.	1241–1341	----------
B-50	do	7°16′ N.	120°45′ E.	2004–2034	16
B-51	5 Dec.	6°57.5′ N.	121°02.5′ E.	0117–0147	3
B-52	do	6°26.5′ N.	120°24′ E.	1022–1122	----------
B-54	do	6°44′ N.	120°06′ E.	2318–2348	----------
B-55	6 Dec.	7°08′ N.	119°27′ E.	0620–0720	3
B-56	do	7°54′ N.	118°51′ E.	1347–1447	17
B-57	do	8°32′ N.	118°20′ E.	2128–2228	24
B-58	7 Dec.	8°00.5′ N.	117°40′ E.	0310–0340	46
B-62	9 Dec.	7°27′ N.	118°15′ E.	1306–1336	6
B-64	10 Dec.	6°48.5′ N.	118°51.5′ E.	1957–2105	10
B-65	11 Dec.	5°57.5′ N.	119°09′ E.	0245–0315	14
B-66	do	5°57′ N.	119°39.5′ E.	0730–0830	30
	1948				
B-94	19 Feb.	7°45.75′ N.	122°06.6′ E.	1220–1250	----------
B-101	23 Feb.	7° N.	123°49′ E.	2010–2110	15
B-102	24 Feb.	6° N.	124° E.	0930–1000	----------
B-103	do	4°55′ N.	124°05′ E.	1850–1920	----------
B-104	25 Feb.	4°58′ N.	124°48′ E.	0232–0302	----------
B-106	do	4°48′ N.	125°30′ E.	1156–1226	----------
B-108	do	5° N.	126° E.	(2)	
B-109	26 Feb.	6° N.	125°48′ E.	0435–0505	----------
B-110	do	6°10′ N.	126°15′ E.	1000–1030	----------
B-112	do	6°22′ N.	125°53′ E.	1525–1555	1
B-113	do	6°44′ N.	125°26′ E.	2026–2056	----------
B-117	1 Mar.	5°18′ N.	125°30′ E.	0150–0220	----------
B-118	do	5° N.	126° E.	1100–1130	----------
B-120	do	3° N.	125° E.	0145–0215	2
B-121	2 Mar.	2° N.	125° E.	0915–0945	----------
B-123	do	2° N.	126° E.	1755–1825	7
B-124	3 Mar.	3° N.	126° E.	0255–0325	11
B-125	do	4° N.	126° E.	1115–1145	----------
B-127	do	4° N.	125° E.	2000–2030	1
B-128	4 Mar.	4° N.	124° E.	0337–0407	----------
B-129	do	3° N.	124° E.	1210–1240	----------
B-131	do	2° N.	124° E.	2150–2220	----------
B-133	7 Mar.	1°06.3′ N.	123°59′ E.	0742–0822	7
B-134	do	1°15′ N.	123°12.5′ E.	1726–1756	----------
B-135	8 Mar.	2° N.	123° E.	0030–0100	----------
B-136	do	3° N.	123° E.	1002–1032	----------
B-138	do	4° N.	123° E.	1805–1835	1
B-139	9 Mar.	5° N.	123° E.	0232–0302	1
B-141	do	6° N.	123° E.	2044–2114	----------
B-150	9 Apr.	3°56′ N.	122°13.5′ E.	0723–0753	----------
B-151	do	3° N.	122° E.	1635–1705	----------
B-152	do	2° N.	122° E.	2255–2325	----------
B-153	10 Apr.	1°14′ N.	122° E.	0555–0625	----------
B-154	do	1°29′ N.	121° E.	1645–1715	3
B-156	do	2° N.	121° E.	2235–2305	14
B-157	11 Apr.	3° N.	120°55′ E.	0650–0720	3
B-158	do	4° N.	121° E.	1535–1705	----------
B-160	12 Apr.	3° N.	120° E.	0200–0230	11
B-161	do	2° N.	120° E.	1035–1105	----------
B-163	do	1° N.	120°05′ E.	2235–2305	----------
B-164	13 Apr.	00°55′ N.	119°08′ E.	0705–0735	----------
B-166	do	2° N.	119° E.	1720–1750	----------
B-167	14 Apr.	3°01′ N.	118°49.5′ E.	0215–0245	----------
B-168	do	3° N.	118°15′ E.	0950–1020	----------
B-170	do	4°04′ N.	118°44′ E.	1801–1831	----------
B-171	15 Apr.	4°08.5 N.	120°06′ E.	0400–0430	4
B-172	do	4°45′ N.	119°54′ E.	1047–1117	----------

See footnotes at end of table.

TABLE 1.—*Station list of larval-fish and plankton tows made in Philippine waters, 1947–49, and number of tuna-like larvae found at each station*—Continued

Station	Date	Latitude	Longitude	Time of tow	Number of specimens
	1948				
B-173	15 Apr.	4°30′ N.	119°30′ E.	1815–1845	----------
B-177	16 Apr.	5° N.	120°30′ E.	2330–2400	1
B-178	17 Apr.	5°05′ N.	121°04.5′ E.	0510–0540	10
B-179	do	5°23′ N.	121° E.	1010–1040	----------
B-183	19 Apr.	5°12′ N.	121°57′ E.	0612–0642	----------
B-185	do	6° N.	122° E.	1342–1412	----------
B-186	do	6°41′ N.	122°23′ E.	1940–2010	5
B-187	20 Apr.	7° N.	123° E.	0205–0235	1
B-188	do	6°57′ N.	122°25′ E.	0605–0635	1
B-240	15 June	12°07′ N.	121°04.5′ E.	1157–1227	----------
B-242	do	11°56.5′ N.	120°45.5′ E.	1625–1655	----------
B-243	16 June	11°41′ N.	121°10′ E.	2142–2212	----------
B-244	do	10°45′ N.	121°48′ E.	0405–0435	1
B-246	do	10°32.5′ N.	121°02′ E.	1630–1700	1
B-248	do	10°17′ N.	120°12′ E.	0645–0715	----------
B-249	17 June	9°23′ N.	122°12′ E.	0645–0715	----------
B-250	do	8°56′ N.	123° E.	1435–1505	3
B-252	do	8°36′ N.	123°04′ E.	1842–1912	----------
B-253	do	8°43′ N.	122°40′ E.	2340–0010	2
B-254	18 June	8°14′ N.	122°07.5′ E.	0620–0650	----------
B-256	do	7°12′ N.	121°05′ E.	1510–1540	----------
B-258	19 June	6°48′ N.	121°26′ E.	1104–1134	1
B-259	do	6°57.5′ N.	129°02.5′ E.	1530–1600	----------
B-260	do	7°45′ N.	121°25′ E.	2245–2315	----------
B-261	20 June	8°20′ N.	120°50′ E.	1613–1643	1
B-263	do	8°51′ N.	121°03′ E.	1500–1530	2
B-264	do	9°27′ N.	120°55′ E.	2300–2330	----------
B-265	21 June	10°04′ N.	120°22′ E.	0600–0630	----------
B-267	do	10°19′ N.	120°03′ E.	1021–1051	----------
B-269	do	9°49′ N.	119°22.5′ E.	1915–1945	----------
B-270	do	9°31′ N.	119°40′ E.	2335–0005	----------
B-271	22 June	9°8′ N.	119° E.	0708–0730	----------
B-273	do	8°27.5′ N.	119° 34′ E.	1432–1502	----------
B-275	do	8°57′ N.	120°15′ E.	2215–2245	----------
B-279	24 June	7°51.5′ N.	120°10′ E.	0030–0100	----------
B-280	25 June	7°16′ N.	119°42′ E.	0817–0847	1
B-293	10 July	6°44′ N.	120°06′ E.	1330–1400	----------
B-294	do	6°26.5′ N.	120°24′ E.	1822–1852	1
B-295	11 July	5°57′ N.	119°56′ E.	0030–0055	1
B-296	do	5°53′ N.	119°23′ E.	0625–0655	1
B-298	do	6°17.5′ N.	118°20′ E.	1320–1350	----------
B-299	do	6°48.5′ N.	118°51.5′ E.	1917–1947	----------
B-300	12 July	7°27′ N.	118°15′ E.	0320–0357	----------
B-301	do	7°35′ N.	117°45′ E.	0845–0915	----------
B-303	do	7°58′ N.	117°11.5′ E.	1555–1625	----------
B-307	14 July	7°55′ N.	116°42′ E.	1110–1140	----------
B-308	do	7°12.2′ N.	116°12.5′ E.	1757–1827	----------
B-309	do	7°26.5′ N.	116°55′ E.	2335–0005	7
B-310	15 July	8°32′ N.	118°20′ E.	1422–1452	----------
B-312	do	7°57′ N.	118°55′ E.	2115–2145	----------
B-313	16 July	7°21′ N.	119°30.5′ E.	0425–0455	----------
B-323	29 July	6°57′ N.	122°25′ E.	0803–0833	----------
B-324	do	6°41.5′ N.	122°24.5′ E.	1055–1125	----------
B-325	do	6° N.	122° E.	1908–1938	----------
B-326	30 July	5°23′ N.	121° E.	0650–0720	----------
B-327	do	5° N.	121° E.	1053–1123	----------
B-329	do	5° N.	120°30′ E.	1555–1625	1
B-330	do	4°45′ N.	119°53′ E.	2130–2200	8
B-331	31 July	4°31′ N.	119°30′ E.	0220–0250	1
B-332	do	4° N.	120° E.	0930–1000	----------
B-333	do	4° N.	118°44′ E.	1817–1847	1
B-335	1 Aug.	3° N.	118°15′ E.	0242–0312	----------
B-337	do	3° N.	119° E.	1010–1040	----------
B-338	do	1°56.5′ N.	119° E.	1802–1832	3
B-339	do	1° N.	119°08′ E.	0202–0232	20
B-340	2 Aug.	1° N.	119°57′ E.	1205–1235	----------
B-342	do	2° N.	120° E.	2130–2200	1
B-343	3 Aug.	2°56′ N.	120° E.	0550–0620	----------
B-345	do	4°05′ N.	120°59′ E.	2055–2125	1
B-346	4 Aug.	3°04′ N.	120°54.5′ E.	0630–0700	----------
B-348	do	2° N.	121° E.	1650–1720	15
B-349	do	1°29′ N.	121° E.	2142–2212	----------
B-350	5 Aug.	1°14′ N.	122° E.	0831–0901	----------
B-352	do	2° N.	122° E.	1536–1606	----------
B-353	do	3° N.	122° E.	0037–0107	16
B-355	6 Aug.	4° N.	122° E.	0845–0915	1
B-356	do	5° N.	122° E.	1652–1722	6
B-358	7 Aug.	7° N.	123° E.	0910–0940	----------
B-375	4 Sept.	7° N.	123°49′ E.	2318–2348	3
B-376	5 Sept.	6° N.	124° E.	0857–0927	1
B-378	do	5° N.	124° E.	1700–1730	1
B-379	do	5° N.	125° E.	0243–0313	12
B-380	6 Sept.	5°18′ N.	125°30′ E.	0943–1013	1
B-382	do	4°48′ N.	125°30′ E.	1430–1500	----------
B-383	do	5° N.	126° E.	2127–2157	3
B-384	7 Sept.	6° N.	125°48′ E.	0607–0637	2
B-386	do	6°10′ N.	126°15′ E.	1058–1128	----------

TABLE 1.—*Station list of larval-fish and plankton tows made in Philippine waters, 1947–49, and number of tuna-like larvae found at each station*—Continued

Station	Date	Latitude	Longitude	Time of tow	Number of specimens
	1948				
					R
B-387	7 Sept.	6°22′ N.	125°53′ E.	1616–1646	1
B-388	do	6°44′ N.	125°46′ E.	2046–2116	2
B-393	10 Sept.	4° N.	126° E.	0832–0902	----------
B-395	do	3° N.	126° E.	1703–1733	----------
B-396	do	2° N.	126° E.	0155–0225	7
B-397	11 Sept.	2° N.	125° E.	1100–1130	----------
B-399	do	3° N.	125° E.	1945–2015	----------
B-400	12 Sept.	4° N.	125° E.	0440–0510	2
B-402	do	4° N.	124° E.	1348–1418	----------
B-403	do	3° N.	124° E.	2355–0025	3
B-404	13 Sept.	2° N.	124° E.	0910–0942	----------
B-405	do	1°08′ N.	124° E.	1635–1705	2
B-407	do	1°13′ N.	123° E.	0045–0115	2
B-408	14 Sept.	2° N.	123° E.	0900–0930	1
B-410	do	2°30′ N.	123°04′ E.	1550–1620	----------
B-411	do	2°56′ N.	123°03.5′ E.	2100–2130	4
B-412	15 Sept.	3°53′ N.	123° E.	0624–0654	----------
B-414	do	5° N.	123° E.	1557–1627	----------
B-415	do	6° N.	123° E.	0120–0150	9
	1949				
B-476	13 Jan.	14°16′ N.	120°31′ E.	1232–1302	----------
B-477	do	14° N.	119°50′ E.	2000–2030	----------
B-479	14 Jan.	14°20′ N.	119°10′ E.	0658–0728	1
B-482	do	14°30′ N.	119°50′ E.	1431–1504	1
B-484	21 Jan.	13°35′ N.	120°07′ E.	2110–2140	25
B-485	22 Jan.	13°24′ N.	119°39′ E.	0230–0300	15
B-486	do	12°42.5′ N.	119°32.5′ E.	0842–0912	4
B-487	do	12°59′ N.	119°56′ E.	1400–1430	1
B-488	do	13°16′ N.	120°21′ E.	1946–2018	4
B-490	23 Jan.	12°50′ N.	120°37′ E.	0257–0327	7
B-492	do	12°32.5′ N.	120°08.5′ E.	1815–1845	1
B-493	do	12°13′ N.	120°33.5′ E.	2255–2325	----------
B-494	24 Jan.	12°24′ N.	120°52.5′ E.	0217–0247	18
B-495	do	12°07′ N.	121°04.5′ E.	0556–0626	101
B-496	do	11°58′ N.	120°49′ E.	0855–0925	----------
B-497	do	11°31′ N.	120°39′ E.	1230–1300	2
B-498	do	11°45.3′ N.	121°11.2′ E.	1734–1804	10
B-499	do	11°43′ N.	121°48′ E.	2318–2348	3
B-500	25 Jan.	10°52.5′ N.	121°51.5′ E.	0602–0632	8
B-501	do	10°56′ N.	120°52.5′ E.	1340–1410	3
B-502	do	10°36′ N.	120°37′ E.	1616–1646	13
B-503	do	10°19′ N.	120°03′ E.	2040–2110	34
B-504	26 Jan.	9°49′ N.	119°22.5′ E.	0302–0332	----------
B-505	do	9°43.5′ N.	118°43.5′ E.	(3)	----------
B-507	27 Jan.	7°33′ N.	120°29′ E.	0405–0435	1
B-509	28 Jan.	6°21′ N.	118°20′ E.	1650–1720	----------
B-510	do	6°56′ N.	118°14′ E.	2058–2128	17
B-512	29 Jan.	7°50′ N.	117°08′ E.	0819–0849	----------
B-515	31 Jan.	7°40.5′ N.	117° E.	0758–0828	1
B-516	do	7°12.5′ N.	116°12.5′ E.	1310–1340	----------
B-517	do	8°07.5′ N.	116°07′ E.	2232–2302	----------
B-518	1 Feb.	7°57′ N.	116°31′ E.	0338–0408	2
B-520	do	9°20′ N.	117°03.5′ E.	1410–1440	----------
B-521	do	9°12′ N.	117°15.5′ E.	1734–1804	----------
B-522	2 Feb.	10°25′ N.	117°46′ E.	0245–0315	----------
B-523	do	10°17′ N.	118°06′ E.	0713–0743	1
B-527	3 Feb.	11°03′ N.	119°03′ E.	0740–0810	5
B-528	do	11°22′ N.	118°39.2′ E.	1229–1259	----------
B-529	do	11°44′ N.	118° E.	1919–1949	307
B-532	14 Feb.	13°47′ N.	120°35′ E.	1604–1634	2
B-533	do	13°35′ N.	120°32′ E.	1905–1935	10
B-534	do	13°37′ N.	120°47′ E.	2210–2240	9
B-535	15 Feb.	13°22′ N.	121°27′ E.	0315–0345	2
B-536	do	13°35′ N.	121°25′ E.	0537–0607	29
B-538	do	13°41′ N.	121°56′ E.	0940–1010	----------
B-539	do	13°06′ N.	122°06′ E.	1547–1617	----------
B-540	do	12°37.5′ N.	121°32.5′ E.	1942–2012	302
B-543	16 Feb.	12°17′ N.	121°30′ E.	1004–1034	24
B-544	do	12°06′ N.	121°40′ E.	1307–1337	8
B-545	do	11°55′ N.	121°50′ E.	1540–1610	4
B-546	do	12°10′ N.	122°20′ E.	2157–2227	----------
B-547	17 Feb.	11°50′ N.	122°36.5′ E.	0220–0250	----------
B-549	do	11°49.5′ N.	123°12′ E.	0740–0810	----------
B-550	do	11°15′ N.	123°21.5′ E.	1150–1220	----------
B-551	do	11°04′ N.	123°48′ E.	1617–1647	1
B-552	do	10°39′ N.	123°42′ E.	1935–2005	14
B-553	do	10°40′ N.	123°32.5′ E.	2130–2200	12
B-554	18 Feb.	9°46′ N.	123°14.8′ E.	0319–0339	3
B-555	do	9°22′ N.	123°27′ E.	0701–0731	----------
B-556	do	9°40′ N.	123°37.5′ E.	1145–1215	----------
B-559	19 Feb.	10°23′ N.	124°09′ E.	1205–1235	2
B-560	do	10°40′ N.	124°38′ E.	1918–1948	5
B-563	20 Feb.	11°33′ N.	124°10′ E.	1407–1437	----------
B-564	do	11°46′ N.	124°39′ E.	1802–1817	----------
B-567	21 Feb.	11°56′ N.	124°11′ E.	0907–0932	----------

See footnote at end of table.

TABLE 1.—*Station list of larval-fish and plankton tows made in Philippine waters, 1947–49, and number of tuna-like larvae found at each station*—Continued

Station	Date	Latitude	Longitude	Time of tow	Number of specimens
	1949				
B-568	21 Feb.	12°18′ N.	124°01′ E.	1203–1233	----------
B-569	21 Feb.	13°07′ N.	124°17′ E.	1926–1956	2
B-570	do	12°55′ N.	124°36.5′ E.	2330–2400	----------
B-574	23 Feb.	12°37′ N.	123°27.3′ E.	1841–1911	2
B-575	do	12°51′ N.	123°29.5′ E.	2108–2138	----------
B-576	24 Feb.	12°30′ N.	122°55′ E.	0240–0310	----------
B-577	do	12°51′ N.	122°47′ E.	0649–0719	2
B-581	25 Feb.	13°24′ N.	122°59′ E.	0943–1013	----------
B-582	do	13°41.5′ N.	122°41′ E.	1300–1330	----------
B-655	17 May	18°37′ N.	122°18′ E.	1725–1755	----------
B-657	do	19°30′ N.	122°40′ E.	0055–0125	----------
B-659	18 May	20°24′ N.	123°13.2′ E.	0930–1000	----------
B-661	do	21°19′ N.	123°31′ E.	1807–1837	2
B-663	19 May	20°12.5′ N.	124°18′ E.	0450–0520	----------
B-667	do	19°11′ N.	125°02′ E.	1520–1550	----------
B-669	do	18°05′ N.	125°47′ E.	0155–0225	----------
B-672	20 May	17°45′ N.	124°43′ E.	1030–1100	----------
B-675	do	17°28′ N.	123°45′ E.	1845–1915	14
B-677	21 May	17°47.5′ N.	122°25′ E.	0525–0555	----------
B-680	do	17°06.5′ N.	122°36.7′ E.	1430–1500	3
B-682	do	16°14′ N.	122°19′ E.	0030–0100	----------
B-684	22 May	16°07.5′ N.	122° E.	0445–0515	1
B-686	do	16°13.8′ N.	122°06′ E.	0625–0655	----------
B-689	23 May	15°18′ N.	121°38′ E.	1845–1915	----------
B-691	24 May	14°30′ N.	122°04′ E.	0125–0155	7
B-695	do	14°52′ N.	122°28.9′ E.	0805–0835	4
B-696	do	15°35′ N.	124°40′ E.	1425–1455	5
B-698	do	15°52.5′ N.	123°42′ E.	2250–2320	----------
B-700	25 May	16°02.6′ N.	124°26.8′ E.	0735–0805	----------
B-703	do	14°49′ N.	124°07′ E.	1800–1830	1
B-705	do	14°19′ N.	123°20′ E.	2400–0030	----------
B-708	26 May	14° N.	124°36′ E.	1132–1202	----------
B-710	do	14°40′ N.	125°25′ E.	2048–2118	----------
B-712	27 May	15°20′ N.	126°12′ E.	0520–0550	----------
B-716	do	16° N.	126°59′ E.	1413–1443	----------
B-718	do	15°12′ N.	127°36′ E.	2245–2315	2
B-721	28 May	14°21′ N.	128°15′ E.	0900–0930	1
B-723	do	13°45′ N.	128°51′ E.	1710–1740	----------
B-725	29 May	12°58′ N.	129°03.2′ E.	0217–0247	----------
B-728	do	12°31′ N.	128°31′ E.	1030–1100	----------
B-730	do	12°10′ N.	127°35′ E.	1905–1935	----------
B-732	30 May	11°50′ N.	126°43′ E.	0300–0330	4
B-735	do	11°31′ N.	125°49′ E.	1153–1223	----------
B-737	do	12°08′ N.	125°43′ E.	1815–1845	----------
B-739	do	12°52′ N.	125°20′ E.	0030–0100	----------
B-741	31 May	13°22′ N.	124°52′ E.	0600–0630	----------
B-744	do	11°52′ N.	123°48′ E.	1320–1350	----------
B-748	3 June	10°51′ N.	129°32′ E.	0050–0120	----------
B-751	4 June	9°48′ N.	129°32′ E.	0940–1010	----------
B-753	do	8°44′ N.	129°32′ E.	1835–1905	----------
B-755	5 June	8°32′ N.	129°32′ E.	0353–0423	----------
B-758	do	7°45′ N.	128°18′ E.	1315–1345	----------
B-760	do	6°48′ N.	129°27′ E.	0005–0035	----------
B-763	6 June	5°45′ N.	129°22′ E.	0931–1001	----------
B-765	do	4°54′ N.	129°17′ E.	1655–1725	----------
B-767	7 June	5°21′ N.	129°13′ E.	0355–0425	----------
B-770	do	5°47′ N.	128°16′ E.	1320–1350	----------
B-772	do	4° N.	127°20′ E.	2130–2200	----------
B-775	8 June	5° N.	126° E.	1217–1247	----------
B-777	do	6°16′ N.	126° E.	2040–2110	----------
B-780	9 June	6°42′ N.	125°46′ E.	0800–0830	----------
B-782	do	6°50.3′ N.	125°35′ E.	1218–1248	----------
B-784	do	6°23.7 N.	125°54′ E.	1655–1725	----------
B-786	do	6°13′ N.	126°02′ E.	2210–2240	----------
B-788	10 June	7°03′ N.	126°25′ E.	0300–0330	----------
B-791	do	7°53′ N.	126°44′ E.	0013–0043	----------
B-794	11 June	5°47′ N.	126°40′ E.	0825–0855	----------
B-796	do	8°44′ N.	127°20′ E.	1610–1640	2
B-798	do	9°26′ N.	127°23′ E.	2358–0028	----------
B-801	12 June	9°26′ N.	126°16.3′ E.	0920–0950	----------
B-803	do	10°18′ N.	126°15′ E.	1548–1618	----------
B-805	do	10°58′ N.	126°02′ E.	2143–2213	----------
B-819	18 July	7°12′ N.	116°12′ E.	0510–0540	1
B-821	do	7°57′ N.	116°31′ E.	1215–1245	----------
B-823	do	8°07.5′ N.	116°07′ E.	1700–1730	5
B-825	19 July	9°20′ N.	117°03.5′ E.	0410–0440	2
B-827	do	9°12′ N.	117°15.9′ E.	0645–0715	3
B-830	do	10°17′ N.	118°06′ E.	1720–1750	1
B-832	do	10°25′ N.	117°46′ E.	2135–2205	13
B-834	20 July	11°22′ N.	118°39.2′ E.	0640–0710	----------
B-837	do	10°55′ N.	119°18.5′ E.	1325–1355	----------
B-838	do	10°50.3′ N.	119°22.5′ E.	1445–1515	----------
B-842	23 July	10°55′ N.	119°18.9′ E.	0750–0820	----------
B-844	do	11°44′ N.	118° E.	2005–2035	----------
B-845	24 July	12°05′ N.	117°03′ E.	0610–0640	----------
B-847	do	12°55′ N.	117°04′ E.	1315–1345	1

TABLE 1.—*Station list of larval-fish and plankton tows made in Philippine waters, 1947–49, and number of tuna-like larvae found at each station*—Continued

Station	Date	Latitude	Longitude	Time of tow	Number of specimens
	1949				
B-849	24 July	12°42′ N.	118°44′ E.	0035–0105	----------
B-852	25 July	12°52′ N.	119°50′ E.	0820–0850	----------
B-854	do	13°18′ N.	120°18′ E.	1425–1455	----------
B-856	do	13°25′ N.	119°50′ E.	2050–2120	----------
B-859	1 Aug.	14°05′ N.	119°22′ E.	0300–0330	----------
B-862	do	13°54′ N.	118°37.5′ E.	0945–1015	----------
B-864	do	13°45′ N.	117°53′ E.	1607–1637	6
B-866	do	13°34′ N.	117°07′ E.	2315–2345	3
B-868	3 Aug.	14°22′ N.	117°08′ E.	0755–0825	4
B-870	do	15°10′ N.	117°11′ E.	1520–1550	----------
B-872	do	16°02′ N.	117°06′ E.	2245–2315	----------
B-874	4 Aug.	16°52′ N.	117°18′ E.	0642–0712	----------
B-877	do	15°57′ N.	118° E.	1610–1640	----------
B-879	do	15°55′ N.	118°52′ E.	2323–2353	----------
B-882	5 Aug.	15°05′ N.	119°50′ E.	0823–0853	2
B-884	do	15°53′ N.	119°36′ E.	1700–1730	----------
B-886	do	16°23′ N.	119°40′ E.	2143–2212	----------
B-888	6 Aug.	16°21′ N.	120°12′ E.	0225–0255	5
B-891	do	17°22′ N.	120°16′ E.	0950–1020	----------
B-893	do	17°37′ N.	119°26′ E.	1733–1753	10
B-895	do	17°52′ N.	118°37′ E.	0050–0120	1
B-898	7 Aug.	17°31′ N.	117°27′ E.	1005–1035	----------
B-900	do	18°08′ N.	117°32′ E.	1513–1543	2
B-902	do	19°03′ N.	118°05′ E.	2222–2252	----------
B-904	8 Aug.	19°25′ N.	119°09′ E.	1737–1807	----------
B-907	do	19°58′ N.	118°36′ E.	1545–1615	----------
B-909	do	20°25′ N.	119°16′ E.	2243–2312	1
B-911	9 Aug.	20°42′ N.	120°04′ E.	0543–0612	1
B-914	do	21°40′ N.	120°50′ E.	1442–1512	----------
B-916	do	21°03′ N.	120°52′ E.	2007–2037	1
B-918	10 Aug.	20°17.6′ N.	120°52′ E.	0532–0602	----------
B-921	do	19°32′ N.	120°52′ E.	1158–1228	1
B-923	do	18°49′ N.	120°54′ E.	1940–2010	----------
B-925	11 Aug.	18°58′ N.	119°47′ E.	0507–0537	1
B-928	do	18°25′ N.	120°23.8′ E.	1140–1210	----------
B-930	do	17°56′ N.	120°11′ E.	1643–1712	4
B-937	25 Aug.	6°02′ N.	120°38′ E.	1530–1600	----------
B-939	do	5°33′ N.	120°14′ E.	2006–2036	----------
B-941	do	5°46′ N.	119°52′ E.	2400–0030	1
B-943	26 Aug.	5°10′ N.	119°25′ E.	0513–0543	135
B-946	do	5°01.5′ N.	119°38′ E.	0753–0823	10
B-948	do	6° N.	119°15′ E.	0107–0137	2
B-950	27 Aug.	6°39′ N.	118°47′ E.	0645–0715	----------
B-953	do	7°23.5′ N.	118°33′ E.	2232–2302	----------
B-955	28 Aug.	7°21′ N.	119°31′ E.	0517–0547	----------
B-958	do	7°48′ N.	120° E.	1050–1120	----------
B-960	do	8° N.	119° E.	1752–1822	----------
B-962	do	8°26′ N.	119°20′ E.	2145–2215	----------
B-964	29 Aug.	8°20.5′ N.	118°14′ E.	0525–0555	----------
B-967	do	9°04′ N.	118°40′ E.	1138–1208	1
B-969	do	9°50′ N.	119°13′ E.	1740–1810	----------
B-971	30 Aug.	10°19′ N.	120°15′ E.	0110–0140	----------
B-974	do	9°13′ N.	121° E.	0840–0910	1
B-976	do	9°09′ N.	120°04′ E.	1553–1623	1
B-980	1 Sept.	8°21′ N.	121° E.	1205–1235	----------
B-982	do	7°14′ N.	120°43′ E.	2010–2040	----------
B-984	2 Sept.	6°45′ N.	120°07′ E.	0206–0236	----------
B-987	do	7° N.	121°29′ E.	1225–1255	----------
B-989	3 Sept.	7°04′ N.	121°51′ E.	1921–1951	----------
B-991	4 Sept.	8°15′ N.	122°29′ E.	0145–0215	1
B-993	do	8°37′ N.	123°04′ E.	0705–0735	1
B-996	do	9° N.	123°03′ E.	1025–1055	1
B-998	do	8°53′ N.	121°47′ E.	1910–1940	1
B-1000	5 Sept.	9°31′ N.	122°15′ E.	0040–0110	7
B-1003	do	10°27′ N.	121°51′ E.	0915–0945	5
B-1005	do	10°21′ N.	121°11′ E.	1440–1510	6
B-1007	do	11°44′ N.	121°48′ E.	0035–0105	1
B-1009	6 Sept.	11°40′ N.	121°11′ E.	0532–0602	----------
B-1012	do	12°35′ N.	120°50′ E.	1234–1304	----------
B-1014	do	12°31′ N.	120°23′ E.	1625–1655	----------
B-1016	12 Sept.	13°37′ N.	120°37′ E.	2215–2245	----------
B-1018	13 Sept.	13°30′ N.	121°31′ E.	0504–0534	----------
B-1022	do	12°30′ N.	121°45′ E.	1220–1250	3
B-1024	do	12°06′ N.	122°22′ E.	1930–2000	----------
B-1028	14 Sept.	12°55′ N.	122°30′ E.	1630–1700	17
B-1030	do	13°29′ N.	122°55′ E.	2155–2225	----------
B-1031	15 Sept.	12°33′ N.	123°33′ E.	0609–0639	----------
B-1034	do	13°07′ N.	124°18′ E.	0030–0100	2
B-1035	16 Sept.	13°08′ N.	124°05′ E.	0310–0340	----------
B-1038	17 Sept.	11°49′ N.	124°10′ E.	2200–2230	----------
B-1040	18 Sept.	10°44′ N.	125°19′ E.	2212–2242	8
B-1042	19 Sept.	9° N.	124°39′ E.	1735–1805	1
B-1043	do	9°35.5′ N.	124°29.2′ E.	2107–2137	----------
B-1045	20 Sept.	9°05′ N.	123°50′ E.	0415–0445	----------
B-1046	do	8°50′ N.	123°57′ E.	0855–0925	1
B-1048	21 Sept.	9°49′ N.	123°15′ E.	0120–0150	----------
B-1050	22 Sept.	10°02′ N.	123°45′ E.	1450–1520	----------

TABLE 1.—*Station list of larval-fish and plankton tows made in Philippine waters, 1947–49, and number of tuna-like larvae found at each station*—Continued

Station	Date	Latitude	Longitude	Time of tow	Number of specimens
	1949				
B-1051	22 Sept.	10°52′ N.	124°12′ E.	2240–2310	1
B-1053	23 Sept.	11°14′ N.	123°19′ E.	0905–0935	----------
B-1057	12 Oct.	13°09′ N.	125°13′ E.	2350–0020	1
B-1060	13 Oct.	14° N.	124°49′ E.	1330–1400	----------
B-1071	16 Oct.	13°38′ N.	128°30′ E.	1445–1515	----------
B-1072	do	13°12′ N.	127°35′ E.	2230–2300	----------
B-1075	17 Oct.	12°18′ N.	125°44′ E.	1415–1445	----------
B-1076	do	11°25′ N.	126°07′ E.	2145–2215	1
B-1077	18 Oct.	10°33′ N.	126°26′ E.	0505–0535	1
B-1079	do	10°43′ N.	127°29′ E.	1333–1403	----------
B-1080	do	10°55′ N.	128°27′ E.	2020–2050	3
B-1081	19 Oct.	11°07′ N.	129°27′ E.	0515–0545	1
B-1083	do	12°14′ N.	130°12′ E.	1450–1520	1
B-1084	do	11°20′ N.	130°36′ E.	2325–2355	----------
B-1085	20 Oct.	10°28′ N.	130°37′ E.	0620–0650	----------
B-1087	do	9°38′ N.	130°38′ E.	1317–1347	----------
B-1088	do	8°44′ N.	130°39′ E.	2005–2035	----------
B-1089	21 Oct.	8°44′ N.	129°40′ E.	0440–0510	----------
B-1091	do	8°44′ N.	128°40′ E.	1120–1150	----------
B-1092	do	8°44′ N.	127°38′ E.	1900–1930	1
B-1093	do	8°44′ N.	126°38′ E.	0405–0435	----------
B-1095	22 Oct.	9°44′ N.	126°38′ E.	1420–1450	----------
B-1105	16 Nov.	12°49′ N.	124°24′ E.	1530–1600	1
B-1106	17 Nov.	14° N.	126°20′ E.	1105–1135	----------
B-1108	18 Nov.	12°10′ N.	124°06′ E.	0936–1006	3
B-1110	do	11°38′ N.	128°38.5′ E.	1540–1610	1
B-1111	19 Nov.	11°23.5′ N.	123°20.7′ E.	0645–0715	1
B-1113	do	11°39′ N.	123°02′ E.	1050–1120	2
B-1114	do	11°56′ N.	123°19′ E.	1425–1455	7
B-1115	20 Nov.	12° N.	122°40′ E.	0845–0915	----------
B-1117	do	11°33′ N.	120°51′ E.	1430–1500	7
B-1118	21 Nov.	10°45′ N.	120°40′ E.	0645–0715	6
B-1120	do	11°21′ N.	120°02′ E.	1255–1325	----------
B-1121	do	11°24′ N.	119°37.5′ E.	1630–1700	----------
B-1123	22 Nov.	10°55′ N.	119°18.3′ E.	1255–1325	----------
B-1124	do	11°06′ N.	118°59′ E.	1615–1645	----------
B-1125	23 Nov.	13° N.	118° E.	0725–0755	----------
B-1127	24 Nov.	13°31′ N.	119°51.2′ E.	(4)	----------
B-1129	do	14°30′ N.	120°45′ E.	1605–1635	----------

[1] Canceled, mechanical trouble.
[2] Sample not taken.
[3] Tow not taken.
[4] Contents not preserved.

The greatest number of tows were made during the month of August. Of 67 hauls, 29 (43.3 percent) were successful. A total of 256 tuna-like larvae was taken, and the average catch for all tows made during August was 3.82 fish. The fewest tows (15) were made during December, with a total of 178 specimens taken in 73.3 percent (11 stations) with an average of 11.8 specimens.

In terms of the number of larvae captured, June was the poorest month. Only 14 specimens were taken in 9 (17.3 percent) of 52 hauls, and the average catch for all tows was 0.27 larvae. The greatest number of larvae were taken in February, when 53 tows resulted in the capture of 764 tuna-like larvae. The number of successful tows was 24 (45.3 percent) of the total operations, and the average catch for all tows was 14.38 fish.

Based on the number of tuna-like larvae collected, December, January, and February are the months of most intensive spawning activity. During these

months, 1,212 larvae were taken in 98 tows. Fifty-six tows (57.1 percent) were successful, with an average of 12.3 specimens per tow for all operations. The number of specimens taken during these 3 months represented 65.8 percent of all specimens captured.

TABLE 2.—*Monthly catch of larval tuna and tuna-like fishes taken by larval-fish and plankton tows in Philippine waters, 1947–49*

Date	Total plankton tows	Plankton tows with tuna larvae		Larvae	
		Number	Percent	Total number	Average catch per tow
1947					
October	21	9	42.8	41	1.95
December	15	11	73.5	178	11.90
1948					
February	10	2	20.0	16	1.60
March	18	7	38.9	30	1.66
April	27	10	37.0	53	1.96
June	27	8	29.6	12	.44
July	25	8	32.0	21	.84
August	17	8	47.0	63	3.70
September	28	17	60.7	56	2.00
1949					
January	30	21	70.0	270	9.00
February	43	22	51.1	748	17.4
May	38	10	26.3	40	1.05
June	25	1	4.0	2	.08
July	18	7	38.9	26	1.44
August	50	21	42.0	193	3.86
September	35	15	42.8	56	1.57
October	20	7	35.0	9	.45
November	16	8	50.0	28	1.75
All	463	192	41.5	1,842	3.97

From this peak of abundance, the number of larvae taken decreased rapidly in March, then gradually declined to its ebb in June. Following the June ebb, the number of larvae captured again increased until a small peak of abundance was reached in August. The number of larvae collected again decreased during the months of September, October, and November.

The distribution of the catch of larval tuna-like fishes according to the hour of the tow is given in table 3. Plankton tows were not conducted at specified times, but usually after each hydrographic station had been occupied. For comparison, day has been designated from 0600 to 1800 hours, and night from 1800 to 0600 hours.

During the daylight hours 250 plankton tows were made, and 212 were made at night. Tuna-like larvae were taken in 87 (34.8 percent) of the day tows and 105 (49.5 percent) in the night hauls. Many more larvae were taken at night than during the day: 1,395 larvae (75.8 percent of the total number) were taken at night, and only 447 (24.2 percent) collected during the day. The average number of specimens from each day tow was 1.78, and from each night tow, 6.58.

TABLE 3.—*Hourly summary of tuna and tuna-like larvae collected in Philippine waters, 1947–49*

Hour	Total plankton tows	Plankton tows with tuna larvae		Larvae	
		Number	Percent	Total number	Average catch per tow
0600–0659	26	9	34.6	126	4.86
0700–0759	18	9	50.0	22	1.22
0800–0859	19	9	47.3	57	2.95
0900–0959	23	7	30.4	13	.56
1000–1059	15	4	26.6	26	1.73
1100–1159	18	3	16.7	4	.22
1200–1259	22	4	18.2	8	.36
1300–1359	19	4	21.0	18	.95
1400–1459	21	8	38.0	50	2.38
1500–1559	16	7	43.7	12	.75
1600–1659	31	14	45.1	59	1.90
1700–1759	22	9	40.9	52	2.36
1800–1859	16	11	68.7	34	2.12
1900–1959	21	10	47.5	657	31.20
2000–2059	16	8	50.0	84	4.62
2100–2159	23	11	47.8	116	5.05
2200–2259	21	8	38.0	46	2.47
2300–2359	17	6	35.3	19	1.12
0000–0059	18	8	44.5	32	1.72
0100–0159	13	8	61.5	29	2.13
0200–0259	21	10	47.6	80	3.80
0300–0359	15	9	60.0	101	6.75
0400–0459	13	6	46.1	12	.92
0500–0559	18	10	55.5	185	10.25

The average catch per hour varied considerably—the most productive hour being from 1900 to 2000 when an average of 31.2 larvae were taken in each tow. Two abnormally large catches, B–529 and B–540, appear to have distorted this average catch, and if they are omitted from the total, the average becomes 2.28 specimens per tow, which conforms more closely to the mean catch of the adjacent hours.

The least productive period during the day was from 0900 to 1600 hours. The average catch per tow during this period was 0.98 larvae, and only 27.6 percent of the 134 tows captured specimens. Early morning, from 0600 to 0700 hours, was the most productive period during the day. An average of 4.86 fish were taken in each of the 26 tows made at this time; 34.6 percent of the tows captured specimens.

The least productive period during the night was from 2300 to 0100 hours, when an average of only 1.45 larvae was obtained in 35 tows; 40 percent of the tows were productive. Disregarding the two apparently abnormally large catches made during the 1900 hour, two periods of large catches occurred during the night. The first occurred from 2000 to 2200 hours, when 200 larvae were taken in 39 tows. The average number per tow was 5.13, with specimens taken in 48.7 percent of total operations. The

second period occurred from 0200 to 0600 hours, when 378 larvae were taken for an average catch of 5.65 fish per tow. During this period 67 tows were made, and 35 (52.2 percent) caught specimens.

Night is not only more productive of specimens, but from the increase in percentage of successful tows, it also seems that the larvae are more widely distributed. Furthermore, there is a considerable vertical migration downward during the day and a return to the surface at night. Since no tows were made beneath the surface, the depth to which tuna-like larvae descend is not known.

Although the exploratory nature of the program over an extensive area precluded the periodic reexamination of any specific area for fluctuations in abundance of tuna-like larvae, sufficient data were collected from 6 irregularly timed trips to the Sulu Sea to indicate possible trends in annual abundance (table 4). Tuna-like larvae were taken in the greatest abundance during December and January, when averages of 11.9 and 12 specimens, respectively, were taken in each haul. The least productive months were June and July, with average catches of 0.44 and 0.66 larvae, respectively.

TABLE 4.—*Summary of larval-fish and plankton tows made during six cruises to the Sulu Sea, 1947–49.*

Month	Total number of tows	Successful tows		Catch, tuna-like larvae		Average surface temperature (centigrade)
		Number	Percent	Total number	Average, all tows	
Jan. 24–31, 1948	16	11	68.8	192	12.00	26.51°
Mar. 22–29, 1949	15	(1)				27.33°
June 15–25, 1948	27	8	29.6	12	.44	29.74°
July 10–16, 1948	15	4	26.7	10	.66	29.28°
Aug. 25–Sept. 6, 1949	32	13	40.1	39	1.22	29.05°
Oct. 7–13, 1947	21	9	42.8	44	1.95	29.30°
Dec. 3–11, 1947	15	11	73.5	178	11.86	28.76°

[1] Biological data not collected during this trip; this entry is included for the surface temperature record.

The surface water temperatures during the trips (table 4) varied from a low of 26.51 °C. in January to 29.74 °C. in June, a range of 3.23 °C. It should be noted that although the temperatures in general were high, the greatest number of tuna-like larvae was collected during the period of lowest temperatures, December and January. The significance of this fact, if any, is not known, but the possibility that the peak of spawning occurs during the period of low temperature should be investigated more completely.

No attempt is made to discuss the ecology of the tuna-like larvae either as a group or by species. These ecological relationships must necessarily await the final analysis of the hydrographic data obtained simultaneously. However, the data of temperature (°C), salinity (°/oo), and phosphates (ug-at/L), as recorded at the surface during each larval-fish and plankton tow, are given in table 5 and contain sufficient information to be of value to future research in this field.

TABLE 5.—*Surface conditions, physical and chemical, at larval-fish and plankton tow stations*

Station No.	Temperature (°C.)	Salinity (o/oo)	Phosphate-P (ug-at/L)	Station No.	Temperature (°C.)	Salinity (o/oo)	Phosphate-P (ug-at/L)
B-5				B-158	29.07	34.27	0.10
B-15	28.87	33.62	0.15	B-160	28.78	34.27	.10
B-16	29.30	32.77	.15	B-161	29.36	34.09	.07
B-17	28.99	33.84	.15	B-163	29.71	34.07	.10
B-18	28.99	33.84	.15	B-164	28.86	33.66	.07
B-20	29.71	33.80	.05	B-166	29.73	34.25	.08
B-21	29.09	33.71	.05	B-167	29.26	34.34	.15
B-22	29.10	33.82	.10	B-168	29.23	34.31	.10
B-23	29.75	33.66	.05	B-170	29.16	34.13	.07
B-24	29.60	33.84	.05	B-171	28.61	34.29	.05
B-25	29.36	33.93	.05	B-172	29.19	34.25	.05
B-26	29.86	33.84	.10	B-173	29.53	34.33	.05
B-27	29.25	33.84	.05	B-177	28.90	34.23	.03
B-28	30.27	33.77	.05	B-178	28.52	34.34	.05
B-29	29.14	33.49	.05	B-179	28.60	34.33	.05
B-31	28.72	33.51	.05	B-183	28.57	34.29	.15
B-32	29.23	33.22	.05	B-185	29.31	34.20	.05
B-33	29.30	33.19	.05	B-186	29.22	34.20	.10
B-34	29.51	33.57	.05	B-187	29.32	34.20	.07
B-35	28.76	33.57	0	B-188	29.26	34.16	.10
B-36	29.03	33.78	.05	B-240	29.94	34.13	.20
B-37	29.51		.05	B-242	30.21	33.73	.13
B-47	28.58	33.26	.20	B-243	30.00	34.11	.10
B-48	28.53	33.58	.10	B-244	29.88	34.07	.08
B-49	28.71	33.98	.05	B-246	30.62	34.02	.10
B-50	28.98	33.06	.03	B-248	30.35	34.20	.10
B-51	28.70	33.08	0	B-249	29.90	34.20	.10
B-52	28.73	33.06	0	B-250	29.68	34.23	.10
B-54	29.08	33.24	0	B-252	30.23	33.86	.05
B-55	28.87	33.87	.05	B-253	30.11	34.09	.05
B-56	28.84	34.02	.05	B-254	29.82	34.02	.05
B-57	28.75	33.96	0	B-256	29.77	33.93	.10
B-58	28.58	33.37	0	B-258	29.62	34.05	.10
B-62	28.97	33.42	.05	B-259	29.85	33.71	0
B-64	28.58	33.49	.05	B-260	29.73	33.91	.05
B-65	28.63	33.13	0	B-261	29.74	34.09	.05
B-66	28.82	33.35	0	B-263	29.37	33.98	.08
B-94				B-264	29.49	34.14	.12
B-101	27.95	34.18	.08	B-265	29.37	34.16	.08
B-102	28.65	34.05	0	B-267	29.26	34.20	.05
B-103	28.40	34.00	.05	B-269	29.30	34.25	.10
B-104	27.39	34.22	0	B-270	29.54	34.18	.10
B-106	27.39	34.24	0	B-271	29.23	34.14	.05
B-108				B-273	29.48	34.02	.08
B-109	26.86	34.51	0	B-275	29.51	34.14	.10
B-110	27.25	34.65	.15	B-279	29.57	34.09	.03
B-112	27.09	34.40	.05	B-280	29.58	34.07	.05
B-113	26.87	34.42	.05	B-293	29.74	34.05	0
B-117	27.31	34.43	.05	B-294	29.66	34.09	.07
B-118	27.59	34.31	.05	B-295	29.01	34.09	.05
B-120	27.75	34.14	0	B-296	28.85	33.96	.10
B-121	27.54	34.07	0	B-298	29.55	33.13	0
B-123	28.08	33.95	0	B-299	29.28	33.10	0
B-124	27.39	34.18	.10	B-300	29.21	32.63	0
B-125	27.69	34.40	0	B-301	29.25	32.70	.03
B-127	27.49	34.40	.10	B-303	29.28	32.57	.03
B-128	27.98	34.25	.05	B-307	29.11	32.63	.05
B-129	28.36	33.80	.05	B-308	29.35	32.21	.03
B-131	28.20	33.93	.05	B-309	29.69	31.74	.07
B-133	28.14	33.80	0	B-310	29.38	32.61	.05
B-134	28.98	33.89	.05	B-312	29.07	33.62	.05
B-135	28.59	33.87	.05	B-313	28.78	33.6	.02
B-136	28.45	34.05	.05	B-323	29.31	33.44	0
B-138	28.56	34.07	.10	B-324	29.11	33.46	.05
B-139	27.90	34.25	.05	B-325	29.05	33.86	0
B-141	28.77	34.13	.10	B-326	29.06	34.05	.08
B-150	28.97	33.89	.05	B-327	29.21	34.09	.05
B-151	29.61	34.29	.05	B-329	29.58	34.16	0
B-152	28.83	34.31	.05	B-330	29.33	34.09	.12
B-153	28.78	34.09	.05	B-331	28.91	33.80	0
B-154	29.33	34.09	.05	B-332	29.27	34.13	0
B-156	29.24	34.22	.05	B-333	29.40	34.05	.03
B-157	28.66	34.29	.05	B-335	28.91	34.05	.05

TABLE 5.—*Surface conditions, physical and chemical, at larval-fish and plankton tow stations*—Continued

Station No.	Temperature (°C.)	Salinity (o/oo)	Phosphate-P (ug-at/L)	Station No.	Temperature (°C.)	Salinity (o/oo)	Phosphate-P (ug-at/L)
B-337	29.27	34.09	0.05	B-538	26.36	34.11	0.08
B-338	29.24	34.09	.05	B-539	26.71	34.22	.05
B-339	28.57	33.91	.05	B-540	26.14	34.09	.05
B-340	28.99	34.09	.10	B-543	26.32	34.13	.05
B-342	29.51	34.09	.05	B-544	25.93	34.09	.10
B-343	29.33	34.13	.05	B-545	25.03	34.11	.15
B-345	29.80	34.16	.05	B-546	26.12	34.09	.05
B-346	29.15	34.11	.05	B-547	26.02	34.22	.05
B-348	30.05	34.05	.15	B-549	25.74	34.33	.05
B-349	29.88	34.04	.15	B-550	26.04	34.27	.15
B-350	28.97	34.05	.15	B-551	25.33	34.16	.20
B-352	29.59	34.09	.05	B-552	25.71	34.14	.20
B-353	29.35	34.23	.08	B-553	26.29	34.13	.05
B-355	29.04	34.20	.15	B-554	25.90	34.16	.15
B-356	29.83	34.22	.15	B-555	25.95	34.31	.10
B-358	29.78	33.33	0	B-556	26.28	34.45	.05
B-375	28.67	33.46	0	B-559	26.44	34.07	.05
B-376	28.61	33.89	.10	B-560	26.37	34.04	.10
B-378	29.28	33.84	0	B-563	26.36	34.20	.05
B-379	28.55	34.25	.07	B-564	26.65	34.07	0
B-380	28.50	34.29	.05	B-567	25.59	34.33	.07
B-382	28.79	34.27	.10	B-568	25.22	34.58	.20
B-383	28.73	34.27	.07	B-569	26.44	34.38	.05
B-384	28.54	34.18	.10	B-570	26.27	34.76	.05
B-386	29.51	34.29	.10	B-574	25.79	34.51	.05
B-387	29.81	34.09	.08	B-575	25.30	34.63	.20
B-388	29.00	33.86	.10	B-576	26.31	34.18	.10
B-393	28.54	34.25	0	B-577	26.28	34.16	.15
B-395	28.41	34.22	.05	B-581	26.25	34.51	.07
B-396	27.68	34.13	.15	B-582	26.37	------	.05
B-397	28.75	34.18	0	B-655	28.92	34.42	0
B-399	29.23	34.22	.05	B-657	28.62	34.31	.05
B-400	28.87	34.27	.10	B-659	28.12	34.37	0
B-402	28.90	34.27	.05	B-661	27.04	34.74	0
B-403	28.95	34.16	.05	B-663	28.01	34.72	0
B-404	28.89	34.13	.05	B-667	28.14	34.87	0
B-405	28.95	34.14	.10	B-669	28.64	34.72	0
B-407	28.77	34.16	.10	B-672	29.01	34.56	.10
B-408	28.91	34.16	.08	B-675	29.21	34.38	0
B-410	------	------	------	B-677	28.23	34.52	0
B-411	28.95	34.16	.12	B-680	29.08	34.29	.05
B-412	28.73	34.25	.10	B-682	29.09	34.42	.05
B-414	28.53	34.33	.15	B-684	30.28	34.23	0
B-415	28.59	33.86	.02	B-686	30.19	34.02	0
B-476	26.43	32.84	0	B-689	30.40	34.09	0
B-477	26.83	32.97	.05	B-691	29.21	34.04	0
B-479	26.64	32.90	0	B-695	28.81	34.67	0
B-482	27.27	33.06	0	B-696	29.76	34.23	.05
B-484	26.35	33.49	.05	B-698	29.20	34.42	.05
B-485	25.35	33.87	.10	B-700	29.23	34.36	.05
B-486	26.03	33.49	.10	B-703	29.23	34.02	0
B-487	26.22	33.60	0	B-705	28.92	34.72	.05
B-488	26.27	33.51	0	B-708	29.07	34.04	0
B-490	26.74	33.49	.05	B-710	29.16	34.42	0
B-492	27.12	33.40	0	B-712	29.03	34.78	0
B-493	26.91	33.44	.05	B-716	29.69	34.54	.05
B-494	26.49	33.64	0	B-718	29.07	34.45	.05
B-495	25.89	33.80	.05	B-721	28.73	34.26	.05
B-496	26.28	33.46	.05	B-723	29.34	34.38	.05
B-497	26.04	33.73	.05	B-725	28.72	34.40	.05
B-498	26.12	33.64	.15	B-728	29.00	34.18	.05
B-499	25.75	33.93	.12	B-730	29.13	34.07	0
B-500	26.54	33.82	.05	B-732	29.01	34.34	.05
B-501	25.98	33.93	.05	B-735	29.14	34.22	0
B-502	25.85	33.93	.05	B-737	29.60	34.25	------
B-503	26.23	33.89	0	B-739	29.02	34.23	.10
B-504	26.97	33.75	0	B-741	29.01	34.25	.05
B-505	------	33.82	.05	B-744	29.83	34.23	0
B-507	27.40	33.82	.05	B-748	28.85	34.31	0
B-509	27.40	33.82	.05	B-751	29.09	34.11	0
B-510	27.13	33.87	.05	B-753	29.34	34.00	.05
B-512	27.07	33.62	0	B-755	28.83	33.98	.15
B-515	26.98	33.80	.15	B-758	29.49	34.07	.05
B-516	26.52	33.35	.10	B-760	29.11	33.87	0
B-517	26.43	33.37	.10	B-763	28.79	33.87	0
B-518	26.43	33.35	.10	B-765	29.54	34.00	.15
B-520	26.84	33.53	.10	B-767	29.80	34.05	.10
B-521	26.59	33.60	0	B-770	29.30	33.46	.05
B-522	26.92	33.21	.05	B-772	29.17	33.98	.05
B-523	26.12	33.49	0	B-775	28.91	34.02	.05
B-527	26.55	33.49	.10	B-777	28.94	33.98	.10
B-528	27.18	32.99	0	B-780	29.08	33.91	0
B-529	27.07	33.13	.10	B-782	29.95	33.77	0
B-532	26.31	33.69	.10	B-784	29.45	33.84	.05
B-533	27.00	33.49	0	B-786	29.24	33.96	.05
B-534	26.52	33.57	.05	B-788	29.10	34.11	0
B-535	26.51	33.82	.04	B-791	29.26	34.20	.05
B-536	26.22	33.96	.05	B-794	29.23	34.13	.15

TABLE 5.—*Surface conditions, physical and chemical, at larval-fish and plankton tow stations*—Continued

Station No.	Temperature (°C.)	Salinity (o/oo)	Phosphate-P (ug-at/L)	Station No.	Temperature (°C.)	Salinity (o/oo)	Phosphate-P (ug-at/L)
B-796	29.55	34.16	0.05	B-980	29.33	33.78	0.05
B-798	29.86	33.93	0	B-982	29.46	33.64	.05
B-801	29.50	34.16	.05	B-984	29.47	33.71	.05
B-803	30.05	34.22	.15	B-987	29.18	33.60	0
B-805	29.73	34.22	.05	B-989	29.19	33.62	.05
B-819	29.31	31.36	0	B-991	29.10	33.78	.05
B-821	29.56	32.00	0	B-993	28.95	33.94	.05
B-823	29.26	32.01	0	B-996	28.64	34.13	.05
B-825	29.39	33.08	0	B-998	29.26	33.63	0
B-827	29.30	33.08	0	B-1000	29.15	33.51	0
B-830	29.62	33.15	0	B-1003	29.28	33.45	0
B-832	29.43	33.13	0	B-1005	29.42	33.22	.05
B-834	29.11	32.97	9	B-1007	28.90	32.68	.05
B-837	30.92	31.47	0	B-1009	29.08	33.48	0
B-838	29.85	30.57	0	B-1012	29.30	32.58	0
B-842	29.65	31.42	0	B-1014	29.52	33.10	0
B-844	29.04	33.49	0	B-1016	29.22	32.83	0
B-845	28.96	33.58	0	B-1018	29.43	34.09	.05
B-847	29.22	33.75	0	B-1022	29.71	33.82	.05
B-849	28.97	33.28	0	B-1024	29.56	33.80	0
B-852	28.66	33.55	0	B-1028	29.71	33.86	0
B-854	28.47	32.79	0	B-1030	29.67	34.04	0
B-856	28.58	33.30	0	B-1031	29.36	34.18	0
B-859	29.14	33.44	0	B-1034	29.46	33.96	.05
B-862	29.49	33.69	0	B-1035	29.18	34.20	.03
B-864	30.01	33.51	0	B-1038	29.15	33.68	0
B-866	29.09	33.33	0	B-1040	29.06	33.44	.05
B-868	29.17	33.31	0	B-1042	29.20	33.93	0
B-870	39.66	33.25	0	B-2043	28.86	34.07	0
B-872	92.54	33.44	0	B-1045	29.28	33.42	.05
B-874	29.27	33.51	0	B-1046	29.24	33.01	.05
B-877	29.55	33.39	0	B-1048	28.93	34.04	.05
B-879	29.40	33.19	0	B-1050	29.86	33.68	0
B-882	29.18	33.10	0	B-1051	29.77	33.60	0
B-884	29.47	30.44	0	B-1053	29.37	33.46	.05
B-886	29.12	31.33	0	B-1057	29.41	34.14	.05
B-888	29.03	29.11	0	B-1060	29.31	34.07	.05
B-891	29.09	32.68	0	B-1071	29.43	34.09	.05
B-893	29.90	33.44	0	B-1072	29.17	34.09	.05
B-895	29.30	33.31	.10	B-1075	29.44	33.93	.05
B-898	29.30	33.46	0	B-1076	28.91	33.98	.05
B-900	28.99	33.31	0	B-1077	28.92	33.98	.05
B-902	28.72	33.40	0	B-1079	28.74	33.98	.05
B-904	28.99	33.37	0	B-1080	28.92	34.09	.05
B-907	28.75	33.40	0	B-1081	28.82	34.02	.05
B-909	28.73	33.40	.05	B-1083	29.04	34.22	.05
B-911	29.14	33.40	0	B-2084	29.92	34.27	.05
B-914	29.25	33.26	0	B-1085	28.85	33.98	.05
B-916	28.93	34.40	0	B-1087	29.11	33.93	.05
B-918	29.26	33.55	.05	B-1088	29.33	33.66	.05
B-921	29.10	34.20	0	B-1089	29.03	33.87	.10
B-923	29.81	32.84	0	B-1091	29.12	33.98	.05
B-925	29.74	33.33	0	B-1092	29.67	34.00	.05
B-928	29.81	33.04	0	B-1093	29.06	33.89	.25
B-930	30.13	33.17	0	B-1095	28.99	33.98	.05
B-937	28.19	34.00	0	B-1102	28.92	32.77	.05
B-939	28.10	33.93	.05	B-1105	27.49	34.43	.08
B-941	27.45	34.02	.05	B-1106	28.59	33.98	.05
B-943	28.34	34.02	.05	B-1108	27.52	33.95	.08
B-946	27.99	34.04	.05	B-1110	28.53	33.95	.05
B-948	28.52	33.95	.05	B-1111	28.26	33.66	0
B-950	28.95	33.78	0	B-1113	28.67	33.31	.05
B-953	29.28	33.86	.05	B-1114	28.78	33.73	.05
B-955	28.98	33.28	0	B-1115	27.84	33.64	.05
B-958	29.30	33.68	.05	B-1117	27.86	33.71	.05
B-960	29.75	33.82	.05	B-1118	28.02	33.53	.05
B-962	29.52	33.73	.05	B-1120	28.65	32.77	.05
B-964	29.47	33.35	.10	B-1121	29.18	32.47	.05
B-967	29.43	32.70	0	B-1123	29.50	27.23	.05
B-969	29.26	33.35	.05	B-1124	28.76	31.83	0
B-971	29.29	33.04	0	B-1125	28.33	33.21	.05
B-974	29.08	33.70	.05	B-1127	28.43	32.92	.05
B-976	29.65	33.64	0	B-1129	28.03	32.27	.25

A number of probable tuna-spawning areas have been determined tentatively by the collection of larval forms. The larger areas (fig. 1), bounded by broken lines, indicate the presence of tuna-like larvae either in consecutive or closely related tows. The small, diamond-shaped areas are those in which a

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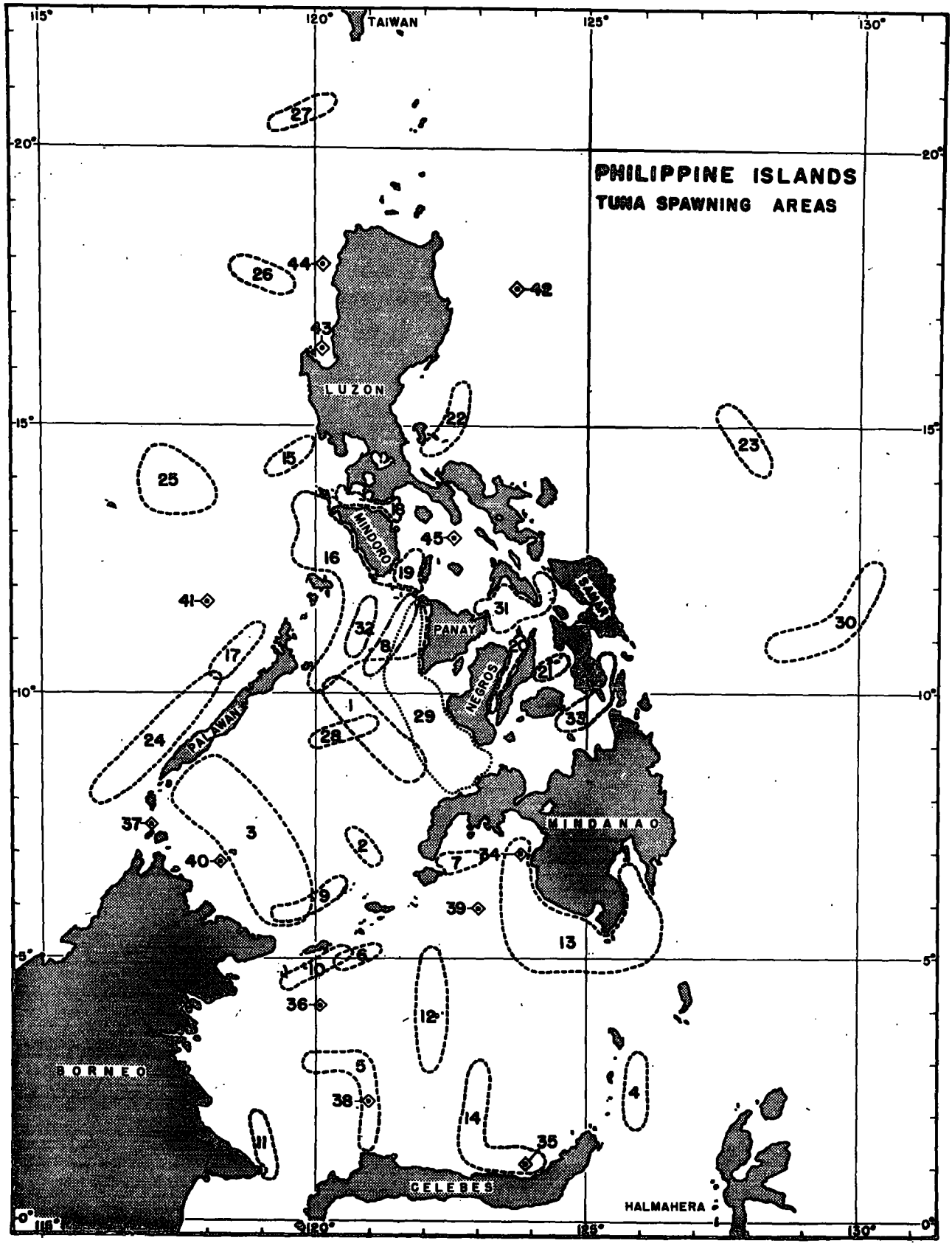
PHILIPPINE ISLANDS
TUNA SPAWNING AREAS
TAIWAN
LUZON
MINDORO
PANAY
NEGROS
SAMAR
PALAWAN
MINDANAO
BORNEO
CELEBES
HALMAHERA
115°
120°
125°
130°
20°
15°
10°
5°
0°

single, isolated haul contained sufficient larvae to seem significant. Each area is identified by a number, and the complete data regarding it are given in table 6. Not included on this chart are those isolated tows in which only very few larvae were taken.

The larvae of some species of tuna-like fishes can be taken throughout the year in Philippine waters, although certain areas seem to be favored. The principal spawning area, as indicated by the collections of the Philippine Fishery Program, is in the northern Sulu Sea and off the west coast of Mindoro Island. Other areas in which considerable numbers of larvae were found are the South China Sea off the west coast of Palawan Island, the southern Sulu Sea, and the south coast of Mindanao Island. Other spawning areas are smaller and more widely scattered, but it should be pointed out that if equal emphasis had been placed upon collecting throughout the archipelago, the distribution would have probably been more uniform.

TABLE 6.—*Principal concentrations of larval tuna and tuna-like fishes found in Philippine waters, 1947–49*

Area and station	Date	Latitude	Longitude	Larvae taken, by genus
Area 1	October 1947			5 *Neothunnus*, 13 *Katsuwonus*, 5 *Euthynnus*.
B-34	Oct. 13	10°02′ N.	120°21. 8′ E.	
B-35	Oct. 13	9°44′ N.	120°38′ E.	
B-36	Oct. 14	9°08′ N.	121°12. 5′ E.	
B-37	Oct. 14	8°32′ N.	121°48. 5′ E.	
Area 2	December 1947			16 *Neothunnus*, 3 *Katsuwonus*.
B-50	Dec. 4	7°16′ N.	120°45′ E.	
B-51	Dec. 5	6°57. 5′ N.	121°02. 5′ E.	
Area 3	December 1947			60 *Neothunnus*, 37 *Katsuwonus*, 46 *Euthynnus*, 7 undetermined.
B-55	Dec. 6	7°08′ N.	119°27′ E.	
B-56	Dec. 6	7°54′ N.	118°51′ E.	
B-57	Dec. 6	8°32′ N.	118°20′ E.	
B-58	Dec. 7	8°00. 5′ N.	117°40′ E.	
B-62	Dec. 9	7°27′ N.	118°15′ E.	
B-64	Dec. 10	6°48. 5′ N.	118°51. 5′ E.	
B-65	Dec. 11	5°57. 5′ N.	119°09′ E.	
B-66	Dec. 11	5°57′ N.	119°39. 5′ E.	
Area 4	March 1948			3 *Katsuwonus*, 6 *Auxis*, 9 *Euthynnus*.
B-123	Mar. 2	2° N.	126° E.	
B-124	Mar. 3	3° N.	126° E.	
Area 5	April 1948			11 *Katsuwonus*, 8 *Euthynnus*, 1 *Auxis*.
B-154	Apr. 10	1°29′ N.	121° E.	
B-156	Apr. 10	2° N.	121° E.	
B-157	Apr. 11	3° N.	120°55′ E.	
B-160	Apr. 12	3° N.	120° E.	
Area 6	April 1948			1 *Katsuwonus*, 1 *Auxis*, 9 *Euthynnus*.
B-177	Apr. 16	5° N.	120°30′ E.	
B-178	Apr. 17	5°05′ N.	121°04. 5′ E.	
Area 7	April 1948			2 *Katsuwonus*, 2 *Auxis*.
B-186	Apr. 19	6°41′ N.	122°23′ E.	
B-187	Apr. 20	7° N.	123° E.	
B-188	Apr. 20	6°57′ N.	122°25′ E.	
Area 8	June 1948			1 *Neothunnus*, 1 undetermined.
B-244	June 16	10°45′ N.	121°48′ E.	
B-246	June 16	10°32. 5′ N.	121°02′ E.	
Area 9	July 1948			1 *Katsuwonus*, 2 undetermined.
B-294	July 10	6°26.5′ N.	120°24′ E.	
B-295	July 11	5°57′ N.	119°56′ E.	
B-296	July 11	5°53′ N.	119°23′ E.	
Area 10	July 1948			1 *Neothunnus*, 6 *Katsuwonus*, 1 undetermined.
B-329	July 30	5° N.	120°30′ E.	
B-330	July 30	4°45′ N.	119°53′ E.	
B-331	July 31	4°31′ N.	119°30′ E.	
Area 11	August 1948			18 *Euthynnus*, 2 *Auxis*, 1 *Neothunnus*, 1 *Katsuwonus*, 1 undetermined.
B-338	Aug. 1	1°56.5′ N.	119° E.	
B-339	Aug. 1	1° N.	119°08′ E.	
Area 12	August 1948			16 *Euthynnus*, 7 undetermined.
B-353	Aug. 5	3° N.	122° E.	
B-355	Aug. 6	4° N.	122° E.	
B-356	Aug. 6	5° N.	122° E.	
Area 13	September 1948			3 *Neothunnus*, 11 *Euthynnus*, 2 *Katsuwonus*, 10 undetermined.
B-375	Sept. 4	7° N.	123°49′ E.	
B-376	Sept. 5	6° N.	124° E.	
B-378	Sept. 5	5° N.	124° E.	
B-379	Sept. 5	5° N.	125° E.	
B-380	Sept. 6	5°18′ N.	125°30′ E.	
B-383	Sept. 6	5° N.	126° E.	
B-384	Sept. 7	6° N.	125°48′ E.	
B-387	Sept. 7	6°22′ N.	125°53′ E.	
B-388	Sept. 7	6°44′ N.	125°46′ E.	
Area 14	September 1948			2 *Katsuwonus*, 2 *Euthynnus*, 5 undetermined.
B-405	Sept. 13	1°08′ N.	124° E.	
B-407	Sept. 13	1°13′ N.	123° E.	
B-408	Sept. 14	2° N.	123° E.	
B-411	Sept. 14	2°56′ N.	123°03.5′ E.	

FIGURE 1.—Spawning areas of tuna and tuna-like fishes in Philippine waters. Broken lines indicate areas in which larvae were taken in two or more consecutive or closely related tows. Diamond-shaped signs indicate isolated, single catches in which a quantity of tuna-like larvae were found.

TABLE 6.—*Principal concentrations of larval tuna and tuna-like fishes found in Philippine waters, 1947–49*—Continued

Area and station	Date	Latitude	Longitude	Larvae taken, by genus
Area 15	January 1949			
B-479	Jan. 14	14°20′ N.	119°10′ E.	1 *Neothunnus*, 1 undetermined.
B-482	Jan. 14	14°30′ N.	119°50′ E.	
Area 16	January 1949			
B-484	Jan. 21	13°35′ N.	120°07′ E.	123 *Euthynnus*, 106 *Auxis*, 2 *Katsuwonus*, 7 undetermined.
B-485	Jan. 22	13°24′ N.	119°39′ E.	
B-486	Jan. 22	12°42.5′ N.	119°32.5′ E.	
B-487	Jan. 22	12°59′ N.	119°56′ E.	
B-488	Jan. 22	13°16′ N.	120°21′ E.	
B-490	Jan. 23	12°50′ N.	120°37′ E.	
B-492	Jan. 23	12°32.5′ N.	120°08.5′ E.	
B-494	Jan. 24	12°24′ N.	120°52.5′ E.	
B-495	Jan. 24	12°07′ N.	121°04.5′ E.	
B-497	Jan. 24	11°31′ N.	120°39′ E.	
B-498	Jan. 24	11°45.3′ N.	121°11.2′ E.	
B-499	Jan. 24	11°43′ N.	121°48′ E.	
B-500	Jan. 25	10°52.5′ N.	121°51.5′ E.	
B-501	Jan. 25	10°56′ N.	120°52.5′ E.	
B-502	Jan. 25	10°36′ N.	120°37′ E.	
B-503	Jan. 25	10°19′ N.	120°03′ E.	
Area 17	February 1949			
B-523	Feb. 2	10°17′ N.	118°06′ E.	6 undetermined.
B-527	Feb. 3	11°03′ N.	119°03′ E.	
Area 18	February 1949			
B-532	Feb. 14	13°47′ N.	120°35′ E.	31 *Euthynnus*, 9 *Katsuwonus*, 1 *Neothunnus*, 11 undetermined.
B-533	Feb. 14	13°35′ N.	120°32′ E.	
B-534	Feb. 14	13°37′ N.	120°47′ E.	
B-535	Feb. 15	13°22′ N.	121°27′ E.	
B-536	Feb. 15	13°35′ N.	121°25′ E.	
Area 19	February 1949			
B-540	Feb. 15	12°37.5′ N.	121°32.5′ E.	334 *Euthynnus*, 4 undetermined.
B-543	Feb. 16	12°17′ N.	121°30′ E.	
B-544	Feb. 16	12°06′ N.	121°40′ E.	
B-545	Feb. 16	11°55′ N.	121°50′ E.	
Area 20	February 1949			
B-551	Feb. 17	11°04′ N.	123°48′ E.	17 *Euthynnus*, 1 *Auxis*, 12 undetermined.
B-552	Feb. 17	10°39′ N.	123°42′ E.	
B-553	Feb. 17	10°40′ N.	123°32.5′ E.	
B-554	Feb. 18	9°46′ N.	123°14.8′ E.	
Area 21	February 1949			
B-559	Feb. 19	10°23′ N.	124°09′ E.	7 undetermined.
B-560	Feb. 19	10°40′ N.	124°38′ E.	
Area 22	May 1949			
B-691	May 24	14°30′ N.	122°04′ E.	2 *Neothunnus*, 1 *Katsuwonus*, 4 *Euthynnus*, 4 undetermined.
B-695	May 24	14°52′ N.	122°28.9′ E.	
B-696	May 24	15°35′ N.	124°40′ E.	
Area 23	May 1949			
B-718	May 27	15°12′ N.	127°36′ E.	1 *Neothunnus*, 2 undetermined.
B-721	May 28	14°21′ N.	128°15′ E.	
Area 24	July 1949			
B-823	July 18	8°07.5′ N.	116°07′ E.	4 *Neothunnus*, 4 *Auxis*, 3 undetermined.
B-825	July 19	9°20′ N.	117°03.5′ E.	
B-827	July 19	9°12′ N.	117°15.9′ E.	
B-830	July 19	10°17′ N.	118°06′ E.	
Area 25	August 1949			
B-864	Aug. 1	13°45′ N.	117°53′ E.	5 *Neothunnus*, 8 undetermined.
B-866	Aug. 1	13°34′ N.	117°07′ E.	
B-868	Aug. 3	14°22′ N.	117°08′ E.	
Area 26	August 1949			
B-893	Aug. 6	17°37′ N.	119°26′ E.	11 *Neothunnus*.
B-895	Aug. 6	17°52′ N.	118°37′ E.	
Area 27	August 1949			
B-909	Aug. 8	20°25′ N.	119°16′ E.	2 *Neothunnus*.
B-911	Aug. 9	20°42′ N.	120°04′ E.	
Area 28	August 1949			
B-974	Aug. 10	9°13′ N.	121° E.	2 *Neothunnus*.
B-976	Aug. 30	9°09′ N.	120°04′ E.	
Area 29	September 1949			
B-991	Sept. 4	8°15′ N.	122°29′ E.	7 *Neothunnus*, 8 *Katsuwonus*, 3 *Euthynnus*, 4 undetermined.
B-993	Sept. 4	8°37′ N.	123°04′ E.	
B-996	Sept. 4	9° N.	123°03′ E.	
B-998	Sept. 4	8°53′ N.	121°47′ E.	
B-1000	Sept. 5	9°31′ N.	122°15′ E.	
B-1003	Sept. 5	10°27′ N.	121°51′ E.	
B-1005	Sept. 5	10°21′ N.	121°11′ E.	
B-1007	Sept. 5	11°44′ N.	121°48′ E.	
Area 30	September 1949			
B-1040	Sept. 18	10°44′ N.	125°19′ E.	8 *Neothunnus*, 1 undetermined.
B-1042	Sept. 19	9° N.	124°39′ E.	
Area 31	October 1949			
B-1080	Oct. 18	10°55′ N.	128°27′ E.	1 *Neothunnus*, 4 undetermined.
B-1081	Oct. 19	11°07′ N.	129°27′ E.	
B-1083	Oct. 19	12°14′ N.	130°12′ E.	
Area 32	November 1949			
B-1108	Nov. 18	12°10′ N.	124°06′ E.	3 *Neothunnus*, 7 *Euthynnus*, 4 undetermined.
B-1110	Nov. 18	11°38′ N.	128°38.5′ E.	
B-1111	Nov. 19	11°23.5′ N.	123°20.7′ E.	
B-1113	Nov. 19	11°39′ N.	123°02′ E.	
B-1114	Nov. 19	11°56′ N.	123°19′ E.	
Area 33	November 1949			
B-1117	Nov. 20	11°33′ N.	120°51′ E.	3 *Neothunnus*, 3 *Auxis*, 7 *Euthynnus*.
B-1118	Nov. 21	10°45′ N.	120°40′ E.	

TABLE 6.—*Principal concentrations of larval tuna and tuna-line fishes found in Philippine waters, 1947–49*—Continued

Area and station	Date	Latitude	Longitude	Larvae taken, by genus
Area 34	February 1948			15 *Euthynnus*.
B-101	Feb. 23	7° N.	123°49′ E.	
Area 35	March 1948			6 *Neothunnus*, 1 *Euthynnus*.
B-133	Mar. 7	1°06.3′ N.	123°59′ E.	
Area 36	April 1948			2 *Neothunnus*, 2 *Katsuwonus*.
B-171	Apr. 15	4°08.5′ N.	120°06′ E.	
Area 37	July 1948			7 *Euthynnus*.
B-309	July 14	7°26.5′ N.	116°55′ E.	
Area 38	August 1948			15 undetermined.
B-348	Aug. 4	2° N.	121° E.	
Area 39	September 1948			8 *Euthynnus*, 1 *Katsuwonus*.
B-415	Sept. 15	6° N.	123° E.	
Area 40	January 1949			17 *Euthynnus*.
B-510	Jan. 28	6°56′ N.	118°14′ E.	
Area 41	February 1949			298 *Euthynnus*, 5 *Katsuwonus*, 3 *Auxis*, 1 *Neothunnus*.
B-529	Feb. 3	11°44′ N.	118° E.	
Area 42	May 1949			12 *Neothunnus*, 2 *Katsuwonus*.
B-675	May 20	17°28′ N.	123°45′ E.	
Area 43	August 1949			5 *Euthynnus*.
B-888	Aug. 6	16°21′ N.	120°12′ E.	
Area 44	August 1949			4 *Neothunnus*.
B-930	Aug. 11	17°56′ N.	120°11′ E.	
Area 45	September 1949			14 *Neothunnus*, 3 *Katsuwonus*.
B-1028	Sept. 14	12°55′ N.	122°30′ E.	

DESCRIPTION OF SPECIES

There are 21 species of tuna and tuna-like fishes found in the Philippine Islands according to Herre (1950). These can be united into 15 genera and either 2, 3, or 4 families, according to the taxonomic authority one accepts. Herre, as well as Jordan (1923), places the so-called scombroid fishes in two families, Scombridae and Thunnidae. The classification used by Berg (1940) created an additional family, Cybiidae, and Kishinouye (1917) placed a portion of the thunnid fishes in a new family, Katsuwonidae. The nomenclature of Kishinouye (1923) has been retained in this publication, in general.

Ten of the 21 species found in Philippine waters are known to occur in some abundance throughout most of the archipelago. The remainder are either quite rare or occur only occasionally. In the family Scombridae, two species of deep-bodied mackerels, genus *Rastrelliger*, are abundant. The family Cybiidae is represented abundantly by *Scomberomorus commerson* and *Gymnosarda nuda*, although occasionally *Sarda orientalis* is taken in considerable quantities. Two species of the family Thunnidae are known to be common, *Neothunnus macropterus* and *Kishinouella tonggol*. There is an abundance of *Katsuwonus pelamis*, *Euthynnus yaito*, *Auxis thazard*, and *Auxis tapeinosoma*, all of the family Katsuwonidae.

An additional species of the family Thunnidae, *Thunnus orientalis*, may occur in some degree of abundance in Philippine waters, but is not found in the commercial catch at the present time. Prior to World War II the Japanese carried on a fishery for this species between northern Luzon and Taiwan (Formosa), but nothing is known of the magnitude of the catch nor the actual extent of the fishing grounds.

The collections made by the Philippine Fishery Program contain the larvae of 5 species of tuna-like fish which can be identified with some degree of accuracy: *Grammatorcynus bicarinatus*, *Neothunnus macropterus*, *Katsuwonus pelamis*, *Euthynnus yaito*, and *Auxis* sp.(?). It has been impossible to separate the two species of the genus *Auxis* known to inhabit Philippine waters, and the description of specimens of this genus may include both species. The larvae of the remaining 16 species of tuna-like fishes are not known at present. Until the larvae of all the so-called scombroid fishes are known, the specific identification of the larval stages of this group will present difficult and complex problems.

The preparation of an adequate description of the several species of larval tunas is a difficult task. The many changes that accompany the rapid growth of the larval forms make illogical any attempt to describe the species using the standard ichthyological technique of proportional measurements and counts. Rather, a general description of each of several sizes of each species, accompanied by adequate illustrations, will be of greater value to future investigations. Several specimens of each species were cleared and stained, using the technique employed by Hollister (1934).

The most complete previous study of tuna and tuna-like larvae was that of Ehrenbaum (1924) who studied collections from the Mediterranean Sea and several portions of the Atlantic Ocean. By his own admission, he could not identify positively every specimen in his possession, and consequently, his results, like the present paper, probably contain some errors. Ehrenbaum explained his lack of positive results as due to the absence of larger larval forms in the collections he studied (which were not obtained during the most favorable season for capturing larvae) and to insufficient knowledge of the morphology and anatomy of the tunas and related species. Although his work has been cited as a general reference, Ehrenbaum's specific identifications have not been used for the most part.

Almost nothing is known concerning the larval forms of tuna and tuna-like fishes found in the Pacific area. The earliest record was made by Lütken (1880) who identified a 17 mm. and a 10 mm. specimen as *Orcynnus* (=*Thunnus*) *germo*. Although no locality record is available for the larger specimen, it probably came from the East Indies, as the vessel from which it was captured was working in that area during the period it was taken, June 3, 1836. The smaller specimen was taken from the South China Sea at an unknown date. It has been suggested by Schaefer and Marr (1948) that these specimens may be the young of *Neothunnus macropterus*. In 1889, Günther, while studying the fish of the *Challenger* expedition, recorded as *Euthynnus yaito* a 0.72-inch thunnid-like specimen taken south of the Caroline Islands in the western Pacific.

The Japanese knowledge of the larval and juvenile forms has been summarized by Kishinouye (1919, 1926). Only a few larval specimens were available in his collections, and his work deals mainly with juveniles. Recently, Schaefer and Marr (1948a, 1948b), Schaefer (1948), Marr (1948), and Wade (1949, 1950) have studied the juvenile stages of this group in the eastern, central, and western Pacific areas. With the exception of Lütken and Kishinouye, no larval specimens have been recorded from the Pacific Ocean until the Philippine Fishery Program of the Fish and Wildlife Service accumulated the collection described herein.

GRAMMATORCYNUS BICARINATUS (Quoy and Gaimard)

Family CYBIIDAE

Genus *Grammatorcynus* Gill

Grammatorcynus Gill, 1862, Proc. Acad. Nat. Sci. Philadelphia, vol. 14, p. 125, orthotype *Thunnus bilineatus* Rüppell.

Grammatorcynus bicarinatus (Quoy and Gaimard)

The species is not common in waters of the Philippines, but it was seen occasionally in small numbers in the public fish markets of Zamboanga, Mindanao, and Jolo, Sulu Archipelago. While it is neither a commercially important nor an abundant species, its identification is another step in the process of distinguishing the larval forms of the tuna and tuna-like fishes inhabiting these waters. The larger of the two specimens illustrated (fig. 3) is not a larval form, but has been included because of its usefulness in identifying the young of this species.

Five of the 8 specimens collected were captured under a night light aboard the experimental fishing vessel *Theodore N. Gill*. Three specimens were taken by the research vessel, *Spencer F. Baird*, 1 under a night light, and 2 in plankton tows.

TABLE 7.—*Station list of* Grammatorcynus bicarinatus *collected in Philippine waters, 1947–49*

Station	Date	Latitude	Longitude	Specimens	
				Number	Size (mm.)
B-29	12 Oct. 1947	6°57′ N.	120°15′ E.	1	8.6
B-339	1 Aug. 1948	1° N.	119°08′ E.	1	12.9
B-345	3 Aug. 1948	4°05′ N.	120°59′ E.	1	8.5
G-65 [1]	3 May 1948	6°04.25′ N.	120°45.5′ E.	4	10–11.5
G-68	6 May 1948	6°43.6′ N.	119°12′ E.	1	17.5

[1] The prefix G refers to stations made by the *Theodore N. Gill*, experimental fishing vessel, Philippine Fishery Program, Fish and Wildlife Service.

The smallest specimen in the collections is 8.5 mm. fork length [2] (fig. 2). The body is deep and heavy. The dorsal outline is almost horizontal from nape to the posterior third of length, then tapers to the slender caudal peduncle. The ventral outline is more or less evenly rounded, anterior to the anal opening. Posterior to the anal opening, the ventral

[2] Fork length is the length from the tip of the snout to the end of the median caudal rays and is used after the caudal fin becomes forked.

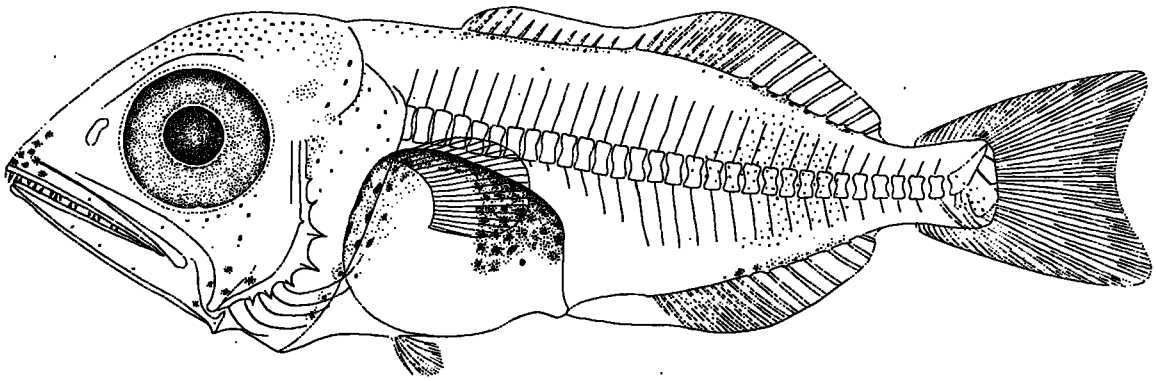

FIGURE 2.—*Grammatorcynus bicarinatus*, 8.5 mm.

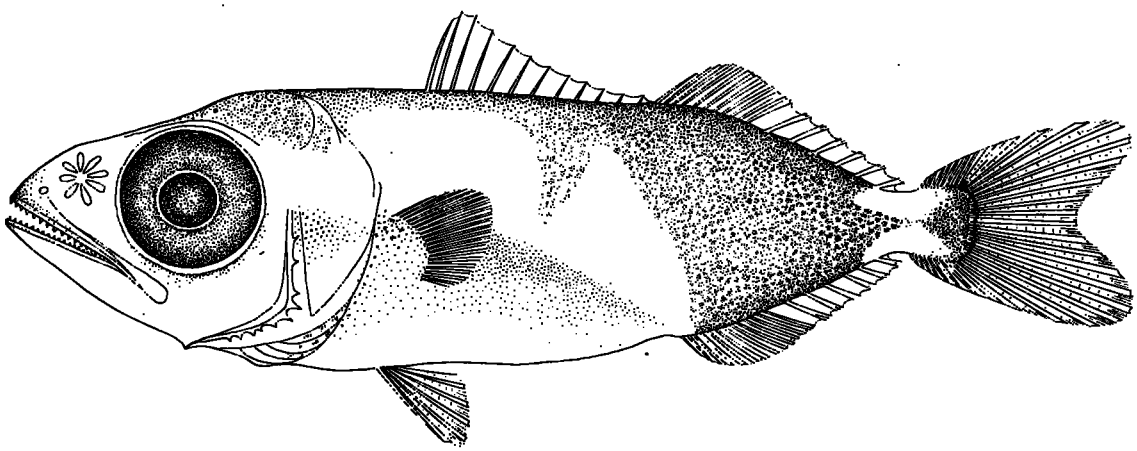

FIGURE 3.—*Grammatorcynus bicarinatus*, 17.5 mm.

outline gradually tapers to the caudal region. The abdominal sac is large, somewhat longer than deep, and the anal opening is about midlength of the body.

The head is large, but not disproportionately so, and its dorsal outline is evenly rounded from above the eye to the tip of the snout. The length of the short, bluntly rounded snout is equal to approximately three-quarters of the eye diameter. The mouth is moderately oblique, and the end of the maxillary extends posteriorly to an imaginary vertical line drawn through the center of the pupil of the eye. The eye is large, almost one-half of the head length. There are eight or nine teeth on each side of both jaws, and the lower jaw is slightly included at the tip.

The development of spines around the edge of the preoperculum is in contrast to the development characteristics of thunnid and katsuwonid larvae which have several long, slender spines at or near the angle of the preoperculum. *Grammatorcynus* spines are all short, heavy, and bluntly pointed. The spine at the angle of the preoperculum is the largest, with three smaller spines along the vertical edge which become progressively smaller dorsally. Three small spines almost equal in size are located along the horizontal edge of the preoperculum. A small spine lies on a faintly marked crest on the surface of the preoperculum. The vertebrae are developed and easily counted in a cleared and stained specimen. There are 13 abdominal vertebrae and 18 caudal vertebrae, a total of 31.

Moderately developed pectoral and small ventral fins are present. The ventral fins are inserted close to the ventral midline beneath the pectoral base. The caudal fin is well developed and slightly forked. The median fins are all present. The first dorsal fin is low, its 13 spines short and weakly developed. The last spine of the first dorsal is almost united with the first ray of the second dorsal. The well-developed second dorsal has 9 rays and 7 finlets, while the anal fin has 11 rays and 7 finlets.

Preserved specimens are light cream in color, with a scattered pattern of small black pigment spots. The dorsal aspect of the head from the nape anteriorly to above the eye is lightly pigmented with small black chromatophores; while laterally, below the nape and behind the eye, there are several scattered areas of similar pigment. There is scattered dark pigmentation on the tip of the snout and immediately posterior to the angle of the jaws. The bases of first dorsal and of both dorsal and anal finlets have a narrow line of dark pigment. A lightly pigmented area extends over the side of the body between the dorsal and anal finlets. There are a few scattered pigment spots at the base of the caudal fin. The abdominal sac is darkly and heavily pigmented dorsally and anteriorly, and the color pattern also extends downward laterally on the posterior portion of the sac.

All other specimens in the collection are larger than 8.5 mm., but show much the same, although more completely developed, characters. The largest specimen, 17.5 mm. fork length, is illustrated in figure 3 principally to show the characteristic color pattern. This color pattern is already faintly evident in the 8.5 mm. specimen, and by the time this species is 10 mm. in length, it is strongly marked.

In the 17.5 mm. specimen, the preopercular spines have developed into a serrated row of 10 short, blunt projections, 6 along the horizontal edge, 1 at the angle, and 3 on the vertical edge. The first dorsal is well developed and the second spine is the longest. Figure 3 is slightly in error with regard to both dorsal and anal finlets for what appears to be the last ray is actually the first finlet. In the specimen it lies close to the last ray, but not as close as the illustration seems to indicate. The second dorsal count is 10 rays plus 7 finlets, and the anal count is 12 rays plus 7 finlets.

G. bicarinatus can be easily separated from the other forms described in this paper by the distinctive color pattern in the larger sizes. Always it can be distinguished by the fewer vertebrae, 31, instead of 39 or 41 as in the other species. The vertebral count is the same as Kishinouye (1923) gave for the deep-bodied mackerel, *Rastrelliger*, but *Grammatorcynus bicarinatus* has 7 dorsal and anal finlets instead of 5, as in *Rastrelliger*.

All of the specimens were taken from the southeastern Sulu Sea and the western portion of the Celebes Sea during the months of May, August, and October.

NEOTHUNNUS MACROPTERUS (Temminck and Schlegel)

Family THUNNIDAE

Genus *Neothunnus* Kishinouye

Neothunnus Kishinouye, 1923, Contributions to the comparative study of the so-called scombroid fishes. Jour. College of Agriculture, Imperial Univ. Tokyo, vol. 8, p. 445, type *Neothunnus macropterus* (Temminck and Schlegel).

Neothunnus macropterus (Temminck and Schlegel)

The smallest recognizable specimen of *Neothunnus macropterus* (fig. 4) in the collections studied is 5.15

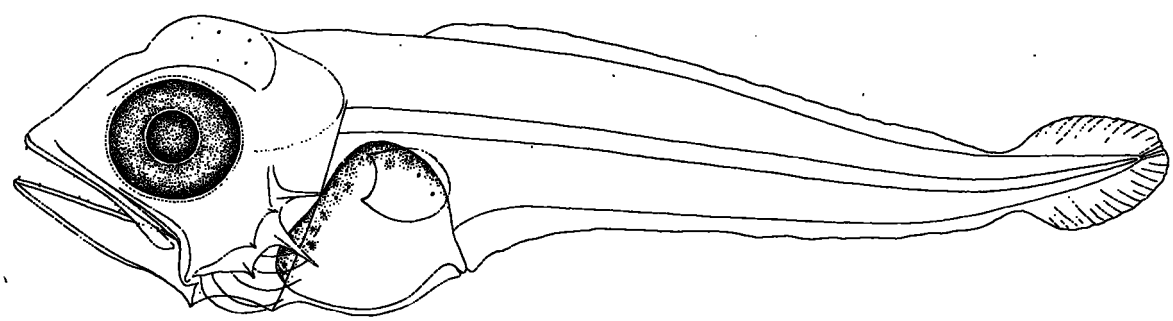

FIGURE 4.—*Neothunnus macropterus*, 5.15 mm.

mm. in total length.[3] This specimen is comparatively long and slender, with its greatest depth immediately behind the eye. The dorsal outline tapers gradually from the greatest depth to the end of the urostyle. The ventral outline is deep and unevenly rounded from the tip of the snout to the anal opening, and then it tapers evenly to the end of the tail.

TABLE 8.—*Station list of larval* Neothunnus macropterus *collected in Philippine waters, 1947–49*

Station	Date	Latitude	Longitude	Specimens	
				Number	Size (mm.)
B-16	7 Oct. 1947	11°07.5′ N.	121°56′ E.	2	6–6.1
B-17	do	10°13′ N.	121°20′ E.	1	5.0
B-34	13 Oct. 1947	10°02′ N.	121°21.8′ E.	5	4.8–5.1
B-50	4 Dec. 1947	7°16′ N.	120°45′ E.	16	6.1–7.8
B-55	6 Dec. 1947	7°08′ N.	119°27′ E.	1	5.2
B-56	do	7°54′ N.	118°51′ E.	10	4.4–6.0
B-57	do	8°32′ N.	118°20′ E.	15	4.8–8.1
B-62	9 Dec. 1947	7°27′ N.	118°15′ E.	6	5–7.5
B-66	11 Dec 1947	5°57′ N.	119°39.5′ E.	28	4–6.8
B-120	1 Mar. 1948	3° N.	125° E.	1	5.4
B-133	7 Mar. 1948	1°06.3′ N.	123°59′ E.	6	5.5–5.8
B-160	12 Apr. 1948	3° N.	120° E.	1	8.3
B-171	15 Apr. 1948	4°08′ N.	120°06′ E.	2	8.4–8.7
B-186	19 Apr. 1948	6°41′ N.	122°23′ E.	3	5.6–6.5
B-246	16 June 1948	10°32.5′ N.	121°02′ E.	1	7.8
B-250	17 June 1948	8°56′ N.	123° E.	3	4–4.5
B-253	do	8°43′ N.	122°40′ E.	2	5.5–7.1
B-263	20 June 1948	8°51′ N.	121°03′ E.	2	8.0
B-331	31 July 1948	4°31′ N.	119°30′ E.	1	7.3
B-338	1 Aug. 1948	1°56.5′ N.	119° E.	1	9.0
B-379	5 Sept. 1948	5° N.	125° E.	1	8.8
B-380	6 Sept. 1948	5°18′ N.	125°30′ E.	1	5.6
B-387	7 Sept. 1948	6°22′ N.	125°53′ E.	1	5.0
B-400	12 Sept. 1948	4° N.	125° E.	1	8.3
B-479	14 Jan. 1949	14°20′ N.	119°10′ E.	1	6.0
B-500	25 Jan. 1949	10°52.5′ N.	121°51.5′ E.	1	5.9
B-529	3 Feb. 1949	11°44′ N.	118° E.	1	7.0
B-536	15 Feb. 1949	13°35′ N.	121°25′ E.	1	(1)
B-675	16 May 1949	17°28′ N.	123°45′ E.	12	5.1–8.5
B-680	21 May 1949	17°06.5′ N.	122°36.7′ E.	2	5.5–6.9
B-696	24 May 1949	15°35′ N.	124°40′ E.	2	6.5–7.4
B-703	25 May 1949	14°49′ N.	124°07′ E.	1	5.0
B-721	28 May 1949	14°21′ N.	128°15′ E.	1	5.2
B-732	30 May 1949	11°50′ N.	126°43′ E.	2	5.5–7.4
B-796	11 June 1949	8°44′ N.	127°20′ E.	1	7.0
B-827	19 July 1949	9°12′ N.	117°15.9′ E.	3	5–5.3
B-830	do	10°17′ N.	118°06′ E.	1	5.6
B-832	do	10°25′ N.	117°46′ E.	13	5.2–9.9
B-847	24 July 1949	12°55′ N.	117°04′ E.	1	6.0
B-866	1 Aug. 1949	13°34′ N.	117°07′ E.	1	6.2
B-868	3 Aug. 1949	14°22′ N.	117°08′ E.	4	5.1–5.5
B-882	5 Aug. 1949	15°05′ N.	119°50′ E.	2	5–5.9
B-893	6 Aug. 1949	17°37′ N.	119°26′ E.	10	4.9–6.2
B-895	do	17°52′ N.	118°37′ E.	1	(1)
B-900	7 Aug. 1949	18°08′ N.	117°32′ E.	2	(1)
B-909	8 Aug. 1949	20°25′ N.	119°16′ E.	1	5.9
B-911	9 Aug. 1949	20°42′ N.	120°04′ E.	1	5.5
B-916	do	21°03′ N.	120°52′ E.	1	11.9
B-921	10 Aug. 1949	19°32′ N.	120°52′ E.	1	9.0
B-925	11 Aug. 1949	18°58′ N.	119°47′ E.	1	5.2
B-930	do	17°56′ N.	120°11′ E.	4	4.9–5.3
B-974	30 Aug. 1949	9°13′ N.	121° E.	1	7.8
B-976	do	9°09′ N.	120°04′ E.	1	4.6
B-993	4 Sept. 1949	8°37′ N.	123°04′ E.	1	7.3
B-1005	5 Sept. 1949	10°21′ N.	121°11′ E.	6	4.8–5.1
B-1022	13 Sept. 1949	12°30′ N.	121°45′ E.	3	4.9–5.2
B-1028	14 Sept. 1949	12°55′ N.	122°30′ E.	14	4.7–8.9
B-1034	15 Sept. 1949	13°07′ N.	124°18′ E.	1	(1)
B-1040	18 Sept. 1949	10°44′ N.	125°19′ E.	8	4.9–6.9
B-1051	22 Sept. 1949	10°52′ N.	124°12′ E.	1	5.0
B-1081	18 Oct. 1949	11°07′ N.	129°27′ E.	1	5.2
B-1092	21 Oct. 1949	8°44′ N.	127°38′ E.	1	6.1
B-1108	18 Nov. 1949	12°10′ N.	124°06′ E.	3	4.7–6.8
B-1118	21 Nov. 1949	10°45′ N.	120°40′ E.	3	5.6–5.9

[1] Distorted.

[3] Total length is the length of the specimen from the tip of the snout to the end of the caudal fin and is used as a measurement of length before the caudal fin becomes forked.

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The abdominal sac is small, anteriorly placed, and slightly longer than high. The anal opening is well forward of the midpoint of the longitudinal axis of the body.

The head is of moderate size, not disproportionately large as in later stages. The snout is short and bluntly pointed, slightly more than half the eye diameter in length. The dorsal outline of the snout is much steeper than the ventral outline. The tip of the snout is even with a horizontal line drawn through the lower edge of the pupil of the eye. The mouth is moderately oblique and large. The end of the maxillary reaches almost to or slightly posterior to a vertical line drawn through the posterior edge of the pupil of the eye. There are 3 to 5 teeth on each side of both jaws. The lower jaw is slightly included at the tip. The nostrils are not evident in specimens of this size.

Three large spines have developed along the edge of the preoperculum. The middle spine, located at the angle, is long, slender, and extends downward and backward over the abdominal sac. The dorsally placed spine is only slightly smaller than the center spine, while the lower spine is much shorter and rather blunt. There are two small blunt spines lying along a slight crest on the preopercular surface. The vertebrae cannot be distinguished, and the urostyle is elongate and bent slightly upward.

The pectoral fins are present, although small and difficult to locate, while the ventral fins remain undeveloped. No median fins are present, but are represented by a low, continuous membrane beginning on the dorsal midline, just behind the base of the pectoral, and extending backward around the caudal tip and forward along the ventral midline to the anal opening. No fin rays are present in the median membrane, although faint streaks are visible in the caudal region.

The color of formalin-preserved specimens is white. A few small black chromatophores are scattered throughout the membrane covering the brain. The peritoneal lining of the abdominal sac is darkly pigmented dorsally and anteriorly.

In somewhat larger specimens, 6.19 to 6.7 mm. (figs. 5 and 6) the body is heavier anteriorly; otherwise, the body shape is much the same as in the smaller specimens. The head is larger and more pronounced in relation to the rest of the body, and the eye has grown relatively smaller as the head has increased in size. The snout is longer, more pointed,

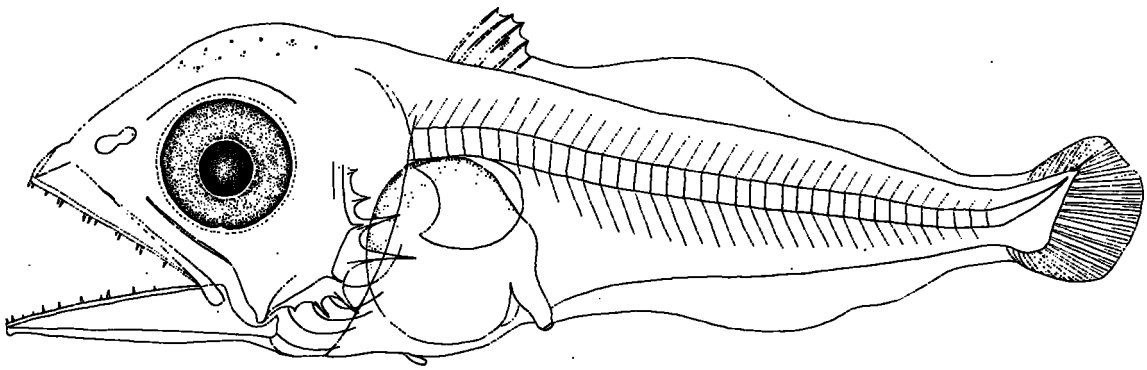


FIGURE 5.—*Neothunnus macropterus*, 6.19 mm.

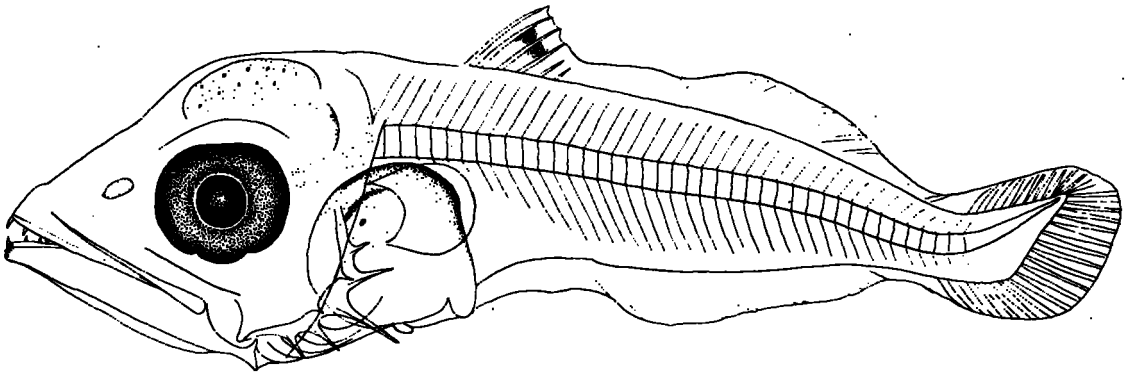


FIGURE 6.—*Neothunnus macropterus*, 6.7 mm.

and is equal to, or slightly greater than, the eye diameter The mouth remains large, and the number of teeth on each side of both jaws has increased to between five and seven. No vomerine or palatine teeth are evident. The mouth is moderately oblique, and the end of the maxillary reaches to a vertical between the center and posterior edge of the eye. The lower jaw is slightly included at the tip.

Five to seven spines have developed along the edge of the preoperculum. Of the three large spines at the angle, the center spine is the longest and most slender. One or two short blunt spines occur on both the vertical and horizontal edges. Two short blunt spines are present on a slight crest of the surface of the preoperculum. The vertebrae are scarcely evident and can be seen faintly in cleared and stained specimens. Approximately 36 vertebrae can be distinguished in the 6.19 mm. specimen, whereas about 38 are evident in the 6.7 mm. example.

Five or six rays have developed in the first dorsal fin, but no rays are yet evident in the second dorsal, anal, pectoral, or ventral fins. The ventral fins can be detected only as small "buds" lying below the base of the pectoral fins. Faint vertical streaks are present in the membrane in the region of the second dorsal and anal fins. The caudal rays are clearly evident.

These specimens retain the white coloration characteristic of the smaller examples. A slight scattered black pigmentation is found on the membrane covering the brain as well as on the anterior and dorsal surfaces of the peritoneum of the abdominal sac. In both of these specimens a small dark area of pigment occupies the center of the first dorsal

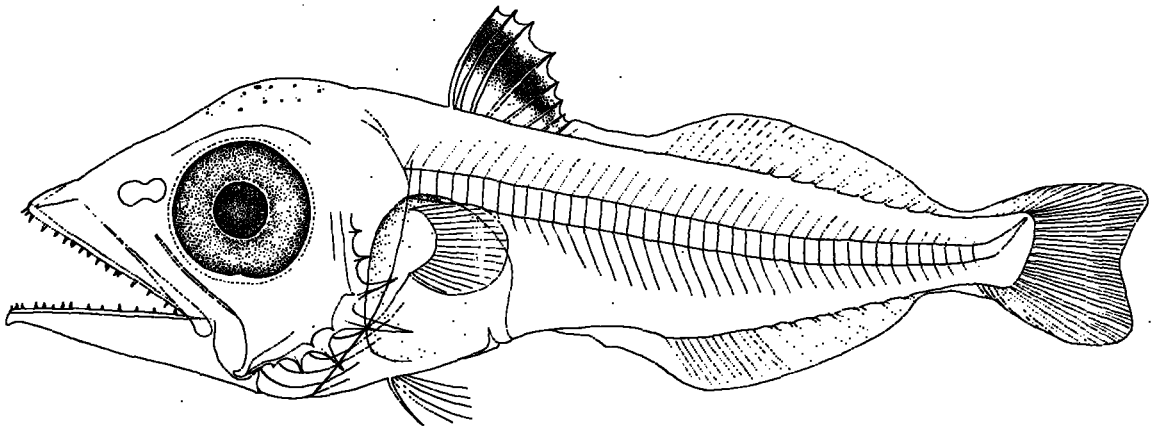


FIGURE 7.—*Neothunnus macropterus*, 7.76 mm.

fin. In the smaller specimen (6.19 mm.) the dark pigmentation is confined to the interradial membrane between two rays, but on the larger (6.7 mm.) the pigmentation is found on two interradial membranes.

A specimen of 7.76 mm. fork length (fig. 7) closely approaches the juvenile form in general appearance. The body depth has increased, especially posterior to the anal opening. The head remains disproportionately large compared to the remainder of the body. The snout is slightly longer and more pointed. The end of the maxillary is placed more anteriorly than in the younger stages, and there are seven or eight teeth on each side of both jaws. Seven spines are present on the edge of the preoperculum, two small spines on the vertical edge, three large spines at or near the angle, and two small spines on the horizontal edge. A third small spine has developed on the slight crest lying on the surface of the preoperculum.

The first dorsal has nine high, well-developed rays. The second dorsal and the anal have 10 and 12 rays, respectively. The beginning of seven dorsal and six anal finlets are faintly discernible. The well-developed caudal fin is forked. The median fins are clearly defined, as the membranes connecting them are degenerating. Both the pectoral and ventral fins are well developed.

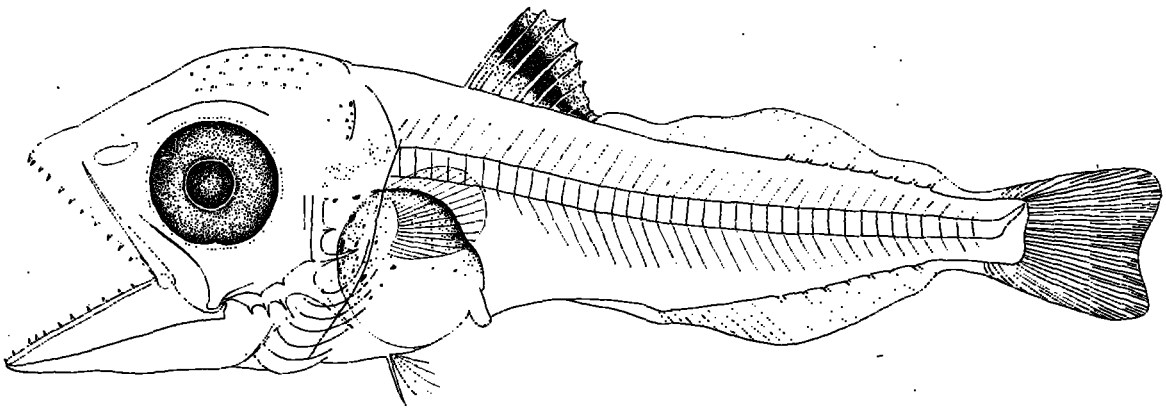


FIGURE 8.—*Neothunnus macropterus*, 8.55 mm.

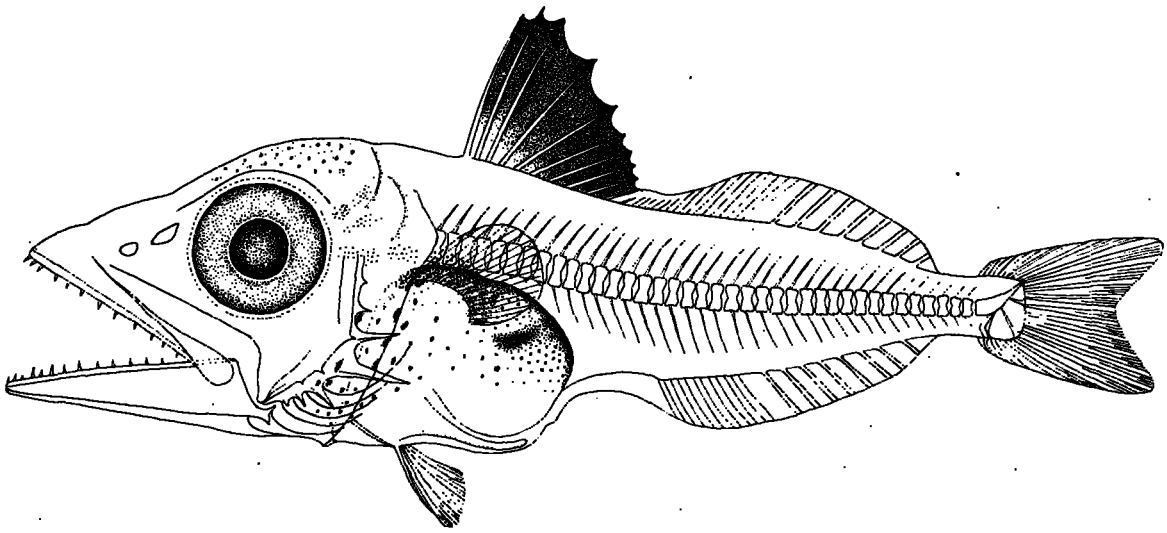


FIGURE 9.—*Neothunnus macropterus*, 9 mm.

Specimens of this length are largely white in color and the only pigmentation occurs on the membrane covering the brain, the peritoneum of the abdominal sac, and the first dorsal fin. The central portion of the first dorsal fin is heavily pigmented with small black chromatophores, and only the distal edge and the basal portion remain colorless.

The body and head have become somewhat deeper and heavier in a 9 mm. fork length specimen (fig. 9) which closely resembles the juvenile form in general appearance. The single nasal opening found in smaller specimens has separated into two pores. The anal opening is placed more posteriorly on the body as the abdominal sac is beginning to extend backward. The formation of the vertebrae is complete, and the hypural plate is developing. Two small palatine teeth are present.

The first dorsal fin with 14 rays, is much higher than the second dorsal, and the longest ray almost reaches the origin of the second dorsal when depressed. The remainder of the fins are well developed.

A somewhat larger specimen of 11.65 mm. fork length is illustrated in figure 10. Several minor differences can be seen between this and the specimen shown in figure 9. The first dorsal fin is lower and has an entirely different outline. The ventral fins are inserted somewhat more posteriorly, slightly behind the origin of the first dorsal fin rather than beneath or slightly anterior to it. Instead of three small spines along the horizontal edge of the preoperculum, there are four. It is not known whether these differences are due to growth or whether they represent valid taxonomic differences.

The fin-ray counts of the two dorsal and anal fins place this specimen in one of three species: *Neothunnus macropterus*, *Thunnus orientalis*, or *Kishinouella tonggol*. It was collected from the waters of Luzon Strait, 21°03′ N., 120°52′ E., which is within the known habitat of *T. orientalis* and from an area of unknown abundance of *N. macropterus* and *K. tonggol*. However, in spite of the possibility that this specimen may be other than *N. macropterus*, it is placed in that species until additional collections more clearly define the related forms.

Specimens of larval *Neothunnus macropterus* longer than 7.5 mm. can be distinguished from the other species described here by the large, highly developed, and almost entirely black first dorsal fin. However, it is quite possible that the unknown larval forms of *Thunnus orientalis*, *Thunnus germo*, and *Kishinouella tonggol* are similar to those of *N. macropterus* and have been included with it. Ehrenbaum (1924) could not separate successfully the larvae of the two common thunnids of the Mediterranean, *Thunnus thynnus* and *Thunnus germo*, on specific differences; therefore, he gave the species name of the more abundant adult to the more abundant larvae.

The early and rapid development of the first dorsal fin, which is first evident in specimens of slightly

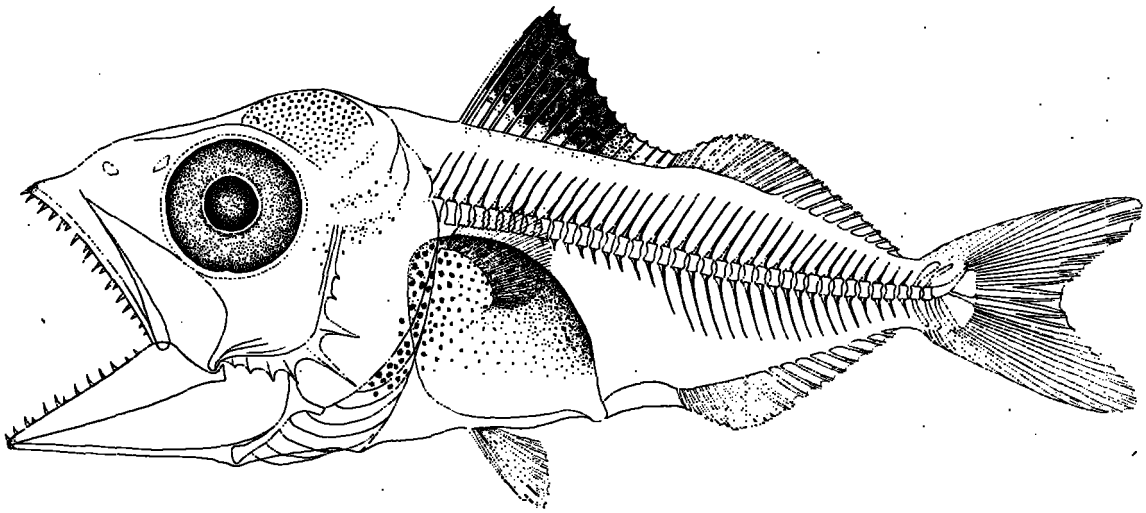


FIGURE 10—*Neothunnus macropterus*, 11.65 mm.

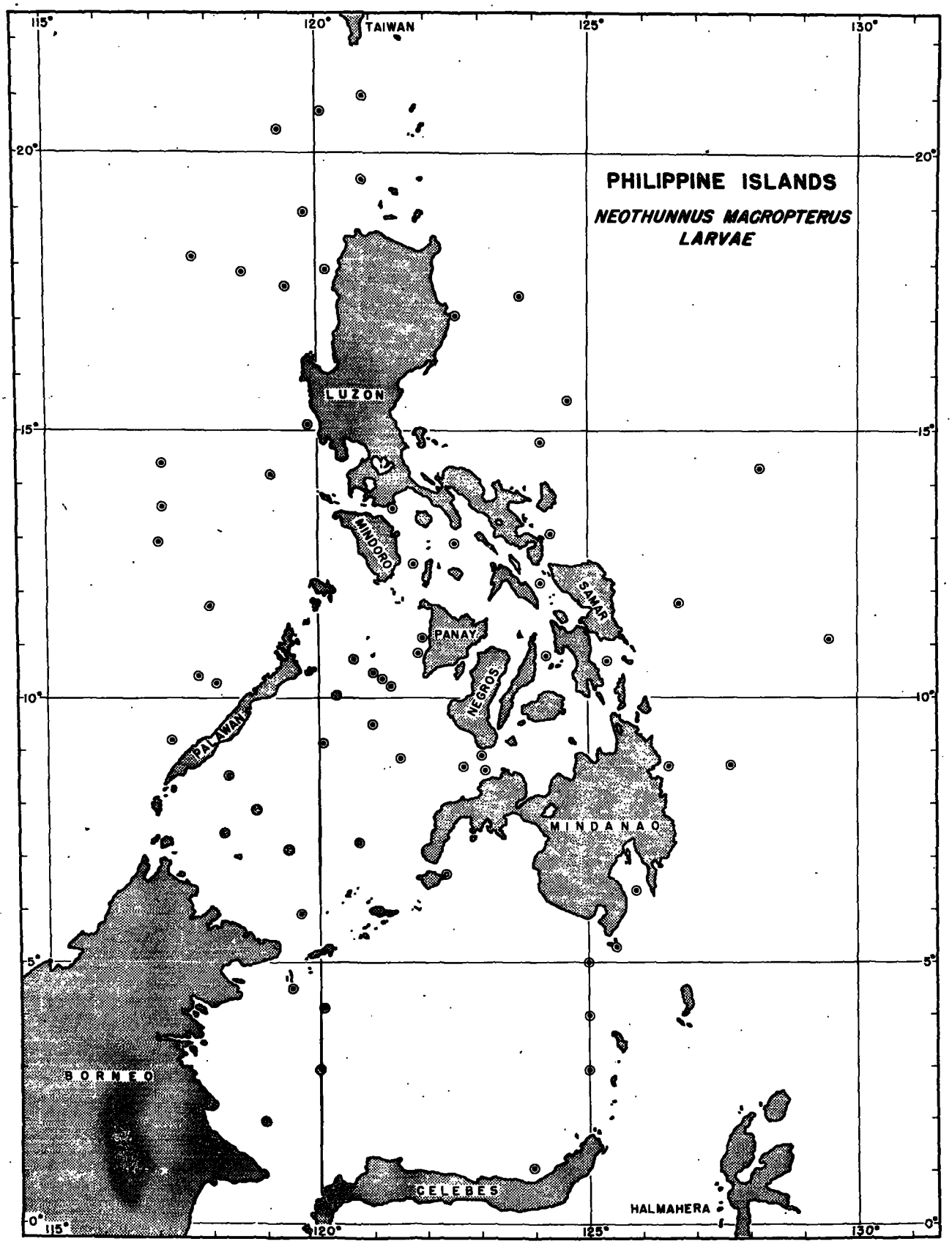
less than 6 mm. length, and the entire absence of black chromatophores on the surface of the body are the principal characters that distinguish this species from about 5.75 to 7 mm. in length. Among the other species described here, only in *Euthynnus yaito* does the first dorsal fin begin to develop at this size. However, *Neothunnus macropterus* can be distinguished from *E. yaito* by the greater height and number of the first dorsal rays present in specimens of equal size. Also, the presence of an irregular series of small pigment spots on the posterior portion of the dorsal and ventral midlines of *E. yaito* is in contrast to the complete lack of pigmented areas on the body of *N. macropterus*.

Few specific characters serve to identify small specimens of *Neothunnus macropterus* 5.5 mm. or smaller, and it is at this size that the judgment and experience of the investigator is used to the greatest extent. The color of these small specimens is white and no pigment spots are present on the surface of the body. The head is moderate in size, and the mouth, only slightly oblique, is not large in relation to the head size. The median fin membranes are moderately to well developed. On many specimens of *Katsuwonus pelamis*, the small pigment spot is absent from the ventral midline of the caudal peduncle, and the surface of the body is colorless as in *N. macropterus*. However, it is distinguished from *K. pelamis* by the very large head, long, pointed snout, and wide gape. Both *Euthynnus* and *Auxis* have some body pigmentation along the posterior portion of the ventral midline and, occasionally, along the dorsal midline in the region of the caudal peduncle.

TABLE 9.—*Monthly catch of larval* Neothunnus macropterus *taken in Philippine waters, 1947–49*

Month	Total number of plankton tows	Tows with larvae		Larvae	
		Number	Percent	Number	Average catch per tow
1947					
October	21	3	14.2	8	0.38
December	15	5	33.3	76	5.05
1948					
February	10				
March	18	2	11.1	7	.39
April	27	3	11.1	6	.22
June	27	4	14.7	8	.30
July	25	1	4.0	1	.04
August	17	1	5.9	1	.06
September	28	4	14.3	4	.14
1949					
January	30	2	6.7	2	.07
February	43	2	4.4	2	.04
May	38	6	15.8	20	.53
June	25	1	4.0	1	.04
July	18	4	22.2	18	1.00
August	50	14	28.0	31	.62
September	35	7	20.0	34	.97
October	20	2	10.0	2	.01
November	16	2	12.5	6	.37
All	463	63	13.6	227	0.49

Larval *Neothunnus macropterus* were taken every month of the year. Unfortunately, none of the spawning areas were reexamined periodically, consequently, variations in abundance of larvae from any one area throughout the year are not known.


PHILIPPINE ISLANDS
NEOTHUNNUS MACROPTERUS
LARVAE
TAIWAN
LUZON
MINDORO
SAMAR
PANAY
NEGROS
PALAWAN
MINDANAO
BORNEO
CELEBES
HALMAHERA
115°
120°
125°
130°
20°
15°
10°
5°
0°

However, based upon the present collections, the period of least catch occurred during January and February. The average catch of all 83 tows made during the 2 months was 0.05 specimen, while only 4 tows (4.8 percent) captured larvae. December yielded the largest average catch for the 15 tows made, 5.06 larvae per tow. Five tows (33.3 percent) contained *Neothunnus* larvae. May, July, August, and September are also indicated as months when *Neothunnus* larvae are more abundant.

Ripening adults of this species were taken by trolling operations throughout the year from the research vessel *Spencer F. Baird* (Wade, 1950b). In addition, a few specimens, with what were judged to be ripe gonads, were captured. A study of the gonad condition of this species made from troll-caught fish suggests that the spawning period is protracted. The present collection of larval forms indicates that this species spawns to some degree throughout the year, and that from March through December it is more intensive than during January and February. The greatest intensity of spawning seems to occur from May through September.

TABLE 10.—*Hourly summary of larval* Neothunnus macropterus *collected in Philippine waters, 1947–49*

Hour	Total number of plankton tows	Tows with larvae		Larvae	
		Number	Percent	Number	Average catch per tow
0600–0659	26	3	11.5	5	0.19
0700–0759	18	3	16.7	30	1.66
0800–0859	19	4	21.1	13	.68
0900–0959	23	2	8.7	4	.17
1000–1059	15	1	6.7	1	.07
1100–1159	18		0		.00
1200–1259	22	2	9.1	4	.18
1300–1359	19	2	10.5	7	.37
1400–1459	21	7	33.3	28	1.33
1500–1559	16	2	12.5	4	.25
1600–1659	31	8	25.2	29	.94
1700–1759	22	2	9.1	11	.50
1800–1859	16	4	25.0	14	.88
1900–1959	21	3	14.3	5	.24
2000–2059	16	2	12.5	17	1.06
2100–2159	23	2	8.7	28	1.23
2200–2259	21	3	14.3	10	.48
2300–2359	17	4	23.5	3	.18
0000–0059	18	1	5.6	1	.06
0100–0159	13	2	15.4	2	.15
0200–0259	21	4	19.1	4	.19
0300–0359	15	1	6.7	2	.13
0400–0459	13	2	15.4	3	.23
0500–0559	18	4	22.2	4	.22

During the daylight hours of 0600 to 1800, 250 larval-fish and plankton tows were made. At night 212 tows were made between 1800 to 0600 hours. Thirty-six hauls (14.4 percent of the day operations) captured larval *Neothunnus macropterus*, and 32 of the night tows (14.5 percent) also caught larvae. During the day an average of 0.54 specimen was taken for all operations, and during the hours of darkness an average of 0.44 specimen was collected.

The hours 0900 to 1300 yielded the poorest catch, and from 2300 to 0400 hours the catch was also low. The greatest hourly average catch of larval *Neothunnus macropterus* was 1.66 specimens for all 18 tows made from 0700 to 0800 hours, although only 16.7 percent of the hauls caught larvae. The highest percentage of successful operations were made from 1400 to 1500 hours when 7 of the 21 tows (33.3 percent) caught larval forms.

The distribution of the percentage of successful operations was almost equal between day and night tows as was the average number of specimens for all day and night hauls. If there is a vertical day and night migration of *Neothunnus macropterus* larvae, it is not evident from these collections. However, during the day it seems likely that fewer larvae are present on the surface from 0900 to 1300 hours than in the early morning or late afternoon. Also, the hours from 2200 to 0400 are less productive of surface fish than the remainder of the night.

KATSUWONUS PELAMIS (Linnaeus)

Family KATSUWONIDAE

Genus *Katsuwonus* Kishinouye

Katsuwonus Kishinouye, 1915, A study of the mackerels, cybiids, tunas. Suisan Gakkai Ho, vol. 1, No. 1, p. 21, type *Scomber pelamis* Linnaeus.

Katsuwonus pelamis (Linnaeus)

The body of *Katsuwonus pelamis* is long and slender in small specimens (fig. 12) of 5 mm. total length. The dorsal and ventral outlines taper gradually and evenly to the end of the caudal fin from the greatest depth which is just posterior to the eye. The head is disproportionately large in relation to the remainder of the body. The head is also bent slightly downward in relation to the body axis. Although this feature does not show clearly in figure 12, it gives the species a characteristic humpbacked appearance. The abdominal sac is small, somewhat rounded, and anteriorly placed. The anal opening is located well forward of the middle of the total length.

FIGURE 11.—Localities in Philippine waters from which the larvae of *Neothunnus macropterus* were collected.

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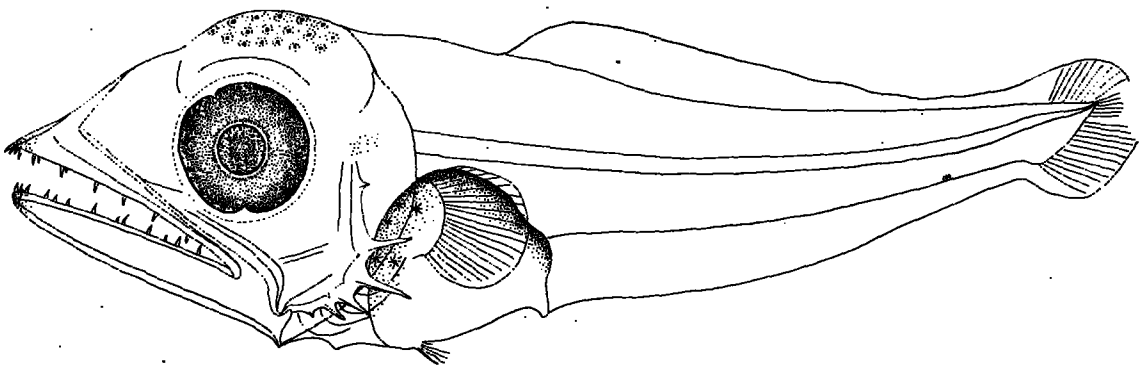


FIGURE 12.—*Katsuwonus pelamis*, 5 mm.

The snout is long and pointed, its tip even with or slightly below the lower edge of the pupil of the eye. The nostrils are not evident. The eye is moderate, its diameter slightly less than the length of the snout. The mouth is large, slightly oblique, and the end of the maxillary reaches a vertical through the posterior edge of the pupil. The lower jaw is slightly included at the tip. There are about eight teeth on each side of both jaws.

TABLE 11.—*Station list of larval* Katsuwonus pelamis *collected in Philippine waters, 1947–49*

Station	Date	Latitude	Longitude	Specimens	
				Number	Size (mm.)
B-17	7 Oct. 1947	10°13′ N.	121°20′ E.	8	5–6.5
B-29	12 Oct. 1947	6°57′ N.	120°15′ E.	4	5.2–5.6
B-35	13 Oct. 1947	9°44′ N.	120°38′ E.	12	4–5.1
B-36	14 Oct. 1947	9°08′ N.	121°12.5′ E.	1	4.7
B-51	5 Dec. 1947	6°57.5′ N.	121°02.5′ E.	3	(1)
B-55	6 Dec. 1947	7°08′ N.	119°27′ E.	2	(1)
B-57	do	8°32′ N.	118°20′ E.	9	4–5.2
B-58	7 Dec. 1947	8°00.5′ N.	117°40′ E.	1	6.4
B-64	10 Dec. 1947	6°48.5′ N.	118°51.5′ E.	9	4.9–6.1
B-65	11 Dec. 1947	5°57.5′ N.	119°09′ E.	14	4.1–6.0
B-66	do	5°57′ N.	119°39.5′ E.	2	5–5.2
B-124	3 Mar. 1948	3° N.	126° E.	3	6–7.6
B-139	9 Mar. 1948	5° N.	123° E.	1	5.5
B-156	10 Apr. 1948	2° N.	121° E.	8	5.5–7.5
B-157	11 Apr. 1948	3° N.	120°55′ E.	3	(1)
B-160	12 Apr. 1948	3° N.	120° E.	9	5–9.1
B-171	15 Apr. 1948	4°08.5′ N.	120°06′ E.	2	5.8–7.0
B-178	17 Apr. 1948	5°05′ N.	121°04.5′ E.	1	5.0
B-186	19 Apr. 1948	6°41′ N.	122°23′ E.	2	5.5–6.0
B-280	25 June 1948	7°16′ N.	119°42′ E.	1	5.9
B-295	10 July 1948	5°57′ N.	119°56′ E.	1	(1)
B-330	30 July 1948	4°45′ N.	119°53′ E.	6	6–7.1
B-338	1 Aug. 1948	1°56.5′ N.	119° E.	1	5.4
B-383	6 Sept. 1948	5° N.	126° E.	2	4.1–4.3
B-396	10 Sept. 1948	2° N.	126° E.	5	4–6.1
B-403	12 Sept. 1948	3° N.	124° E.	2	4.1–4.8
B-411	14 Sept. 1948	2°56′ N.	123°03.5′ E.	2	6–7.7
B-415	15 Sept. 1948	6° N.	123° E.	1	6.0
B-485	22 Jan. 1949	13°24′ N.	119°39′ E.	2	7.1–7.6
B-518	1 Feb. 1949	7°57′ N.	116°31′ E.	1	7.0
B-529	3 Feb. 1949	11°44′ N.	118° E.	5	6.5–8.5
B-536	15 Feb. 1949	13°35′ N.	121°25′ E.	9	5.4–6.8
B-569	21 Feb. 1949	13°07′ N.	124°17′ E.	2	6–7.0
B-675	20 May 1949	17°28′ N.	123°45′ E.	2	6.8–7.2
B-691	24 May 1949	14°30′ N.	122°04′ E.	1	6.1
B-732	30 May 1949	11°50′ N.	126°43′ E.	2	5–5.1
B-796	11 June 1949	8°44′ N.	127°20′ E.	1	7.2
B-941	25 Aug. 1949	5°46′ N.	119°52′ E.	1	7.3
B-991	4 Sept. 1949	8°15′ N.	122°29′ E.	1	5.2
B-998	do	8°53′ N.	121°47′ E.	1	5.0
B-1000	5 Sept. 1949	9°31′ N.	122°15′ E.	5	5.8–6.2
B-1003	do	10°27′ N.	121°51′ E.	1	6.0
B-1028	14 Sept. 1949	12°55′ N.	122°30′ E.	3	(1)
B-1057	12 Oct. 1949	13°09′ N.	125°13′ E.	1	5.0
B-1105	16 Nov. 1949	12°49′ N.	124°24′ E.	1	6.9

[1] Distorted.

Six spines are developed along the edge of the preoperculum: Two long slender spines at the preopercular angle, one a small spine on the vertical edge of the preoperculum, and 3 small spines along the horizontal edge. There are 3 small blunt spines along a slight crest on the surface of the preoperculum. The vertebrae are not developed and the long, slender urostyle is bent slightly upward.

The pectoral fins are present, as are small, undeveloped ventrals. The median fins are not formed, but are represented by a well-developed membrane extending backward along the dorsal midline from above the pectoral base, around the caudal end of the body, and anteriorly along the ventral midline to the anal opening. No fin rays are evident, but faint vertical streaks can be seen in the membrane of the caudal region.

The body color of formalin-preserved specimens is white. The membrane covering the brain is pigmented with scattered, small black chromatophores. The peritoneum of the abdominal sac is densely covered dorsally and anteriorly with small black pigment spots. A small, faintly pigmented area is sometimes found on the side of the head directly behind the eye. In most specimens there is one small black chromatophore on the ventral midline immediately anterior to the caudal peduncle. The tips of the jaws are slightly pigmented.

Only slight changes have taken place by the time this species has reached about 7 mm. total length

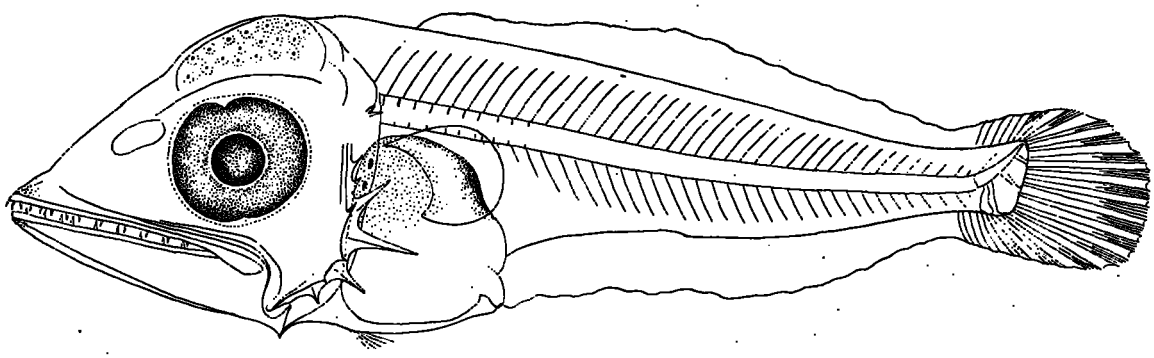


FIGURE 13.—*Katsuwonus pelamis*, 7.15 mm.

(fig. 13). The general appearance of the body remains much the same, although it is slightly deeper and heavier, and the head remains disproportionately large. A single large nostril can be seen on each side of the long pointed snout. Each side of both jaws bears 10 to 12 small pointed teeth. The beginnings of the anterior vertebrae can be seen faintly, and the hypural plate has begun to develop. All of the fins remain undeveloped except for the caudal, which by now has well-defined rays. The color pattern remains the same.

The pectoral and ventral fins are moderately developed. The caudal fin is well developed and slightly forked. The first dorsal has 9 short rays, but the rays and finlets of the second dorsal and anal fins can barely be discerned. There are 11 second-dorsal rays and 5 finlets, and 10 anal rays and 5 finlets developed at this stage. The median fin membrane is degenerating between the two dorsal fins on the caudal peduncle, and between the anal fin and the anal opening.

The body color of formalin-preserved specimens is white or light tan. The usual dark pigmentation is present on the head, on the abdominal sac, and on the ventral midline immediately anterior to the caudal peduncle.

Specimens of approximately 9 mm. fork length (fig. 15) are quite similar to those of 8 mm. The body is more robust and is approaching the juvenile form. The head remains large in relation to the rest of the body. The snout is somewhat longer and more pointed. The single nostril on each side of the snout has almost completely divided into an anterior and posterior nostril. The mouth is large, and there are from 16 to 18 teeth on each side of both jaws.

The development of this species is seemingly quite rapid between the 7.15 (fig. 13) and the 8.2 mm.

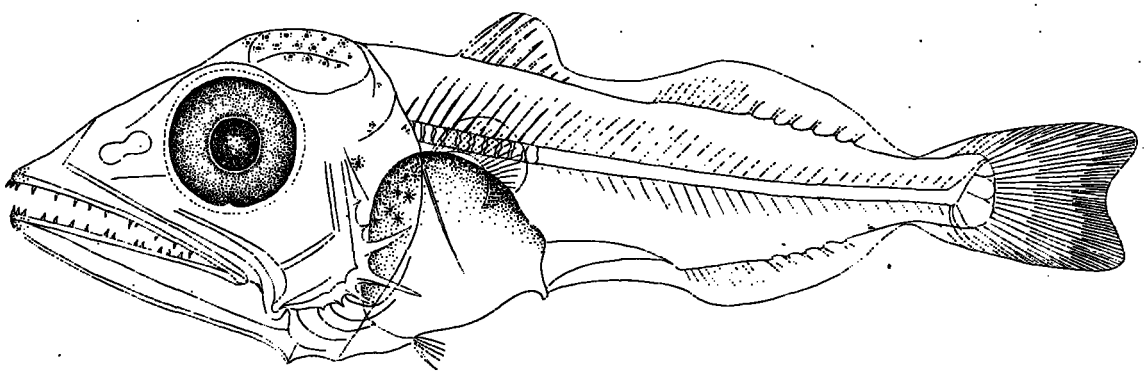


FIGURE 14.—*Katsuwonus pelamis*, 8.2 mm.

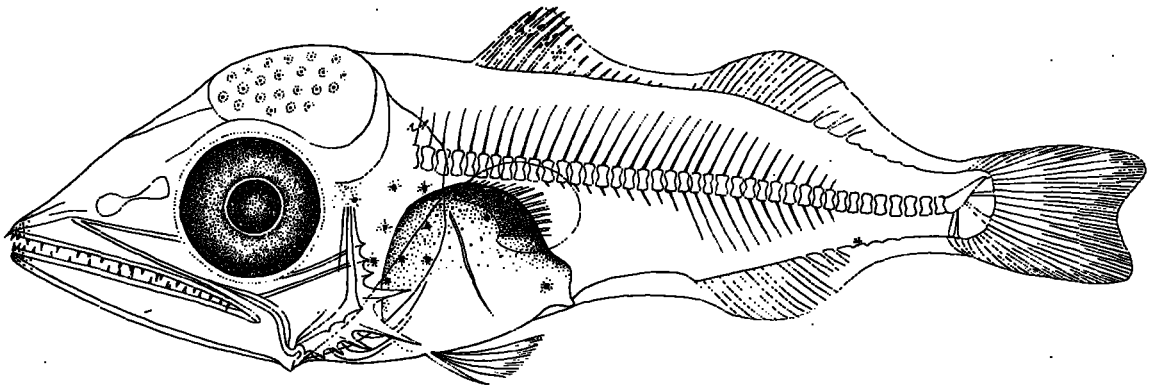


FIGURE 15.—*Katsuwonus pelamis*, 9.1 mm.

fork length specimens (fig. 14), which latter was selected to represent the next stage of development. The body is deeper and heavier, becoming more typically fish-like in appearance. The head remains large and is bent downward in relation to the body axis. The anal opening is placed more posteriorly toward the center of the body.

The long pointed snout has a single nostril on each side which is becoming slightly constricted at the center. The eyes are large, the diameter slightly less than the length of the snout. The mouth is large, slightly oblique, with 10 to 13 teeth on each side of both jaws. Three or four palatine teeth are present. The maxillary extends posteriorly to a vertical line drawn midway between the posterior edge of the pupil and the posterior edge of the eye. The lower jaw is slightly included at the tip.

In the 8.2-mm. specimen (fig. 14) the edge of the preoperculum bears 7 spines. The spine at the angle is long and slender and extends downward and backward over the anterior part of the abdominal sac. The spine immediately above that at the angle of the preoperculum is slightly shorter and heavier and extends slightly upward and backward. There are two small spines on the vertical edge of the preoperculum and three along the horizontal edge. A slight crest on the surface of the preoperculum has three small spines. The developing vertebrae can be faintly seen anteriorly, as can the hypural plate at the base of the caudal.

The 9-mm. specimen (fig. 15) has eight spines along the edge of the preoperculum: Three small spines on the vertical edge, two long slender spines at the angle, and three small spines along the horizontal edge. A slight crest on the surface of the preoperculum has three small spines, and two small temporal spines are present. The vertebrae and the hypural plate are well developed.

The first dorsal has 14 rays, the second dorsal has 15 rays and 8 finlets which can be seen faintly. The anal fin has 13 rays and 7 barely discernible finlets.

The body color remains the same as in smaller specimens with the usual black pigmentation on the head, abdominal sac, and ventral midline. In addition, the first dorsal fin possesses a few scattered small pigment spots on the outer portion of the membrane.

No difficulty was experienced in separating the larvae of *Katsuwonus pelamis* from the larvae of other species described in this publication. In all sizes the disproportionately large head in relation to the remainder of the body serves to identify *K. pelamis* almost positively. In addition, several characteristics of the head, such as the long pointed snout and large gape, are useful in determining the species. The horizontal axis of the head is bent slightly downward in relation to the body axis, which gives this species a somewhat humpbacked appearance. In many, if not most, specimens, one small black pigment spot is present along the ventral midline in the region of the caudal peduncle. Only one other species described in this publication, *Neothunnus macropterus*, has a body surface without pigmentation. The large head of *K. pelamis* separates it from *N. macropterus* when the pigment spot is absent in the former.

Kishinouye (1926) described six specimens, 3 to 6 mm. in length, of what he considered to be *Katsuwonus pelamis*. The specimens were collected during late May and early June 1924, from off Satsunan Shichito, Japan (lat. 28° to 31° N., long. 129° to 131° E.). Two of these specimens, which in his opinion had just hatched, were 3 mm. long. Illustrations are not available in the translation of Kishinouye's work consulted, but from the description, at least one of the specimens with a dorsal and ventral row of chromatophores on the body does not seem to have been *K. pelamis*. The three 4 mm. specimens and the single 6 mm. example quite probably were *K. pelamis*, as he noted the large head and single large chromatophore on the ventral midline just anterior to the caudal peduncle. The smallest specimen which Kishinouye could identify positively was 26 mm. long and was taken from the stomach of an adult *K. pelamis*. In fact, most of his juveniles were taken from the stomachs of adult *K. pelamis* and other pelagic fishes.

TABLE 12.—*Monthly catch of larval* Katsuwonus pelamis *taken in Philippine waters, 1947–49*

Month	Total number of plankton tows	Tows with larvae		Larvae	
		Number	Percent	Number	Average catch per tow
1947					
October	21	4	19.0	25	1.19
December	15	7	46.7	40	2.66
1948					
February	10				
March	18	2	11.1	4	.22
April	27	6	22.1	25	.92
June	27	1	3.7	1	.04
July	25	2	8.0	7	.28
August	17	1	5.9	1	.06
September	28	5	17.8	12	.43
1949					
January	30	1	3.3	2	.06
February	43	4	9.3	17	.39
May	38	3	7.9	5	.13
June	25	1	4.0	1	.04
July	18				
August	50	1	2.0	1	.02
September	35	5	14.3	11	.31
October	20	1	5.0	1	.05
November	16	1	6.2	1	.06
All	463	45	9.7	154	0.33

Specimens of larval *Katsuwonus pelamis* were collected throughout the year as a basis for the present study, with the greatest numbers occurring during the fall, winter, and spring months. The summer months were the least productive; however, it should be noted that larval specimens of this species were never abundant. The largest average number of specimens collected for all operations occurred in December, when an average of 2.66 *K. pelamis* larvae were caught in a total of 15 tows, with 7 tows (46.7 percent) successful. August produced the least *K. pelamis* larvae, when only 2 specimens were captured in a total of 67 hauls for an average of 0.03 specimen. Only 3 percent, or 2 hauls out of the 67, caught specimens.

The capture of the larvae of *Katsuwonus pelamis* throughout the year confirms a previous conclusion, based upon an analysis of troll-caught adults (Wade, 1950b), that this species spawns throughout the year. Although the collections furnish no positive information about the fluctuations in abundance of larvae in any particular area throughout the year, there are indications that the period from September to April, inclusive, may be the principal spawning period. However, the periods of low catch may have been due to operations in areas where *K. pelamis* never spawns in any abundance, and larvae may have been abundant in other areas not sampled.

An outstanding characteristic of the collection of larval *Katsuwonus pelamis* is the great difference between the results of the day and night tows. Only 3.6 percent, or 9 of the 250 day tows, captured larvae, and only 15 specimens were taken for an average of 0.06 specimen for all tows. Night tows, on the other hand, were 17 percent successful, as 36 out of 212 operations caught 139 larvae for an average of 0.66 specimen for the total number of tows made. This indicates a downward migration below the surface during the day and a return to the surface at night. Since only surface tows were made, it is not known to what depths the larvae of this species descend.

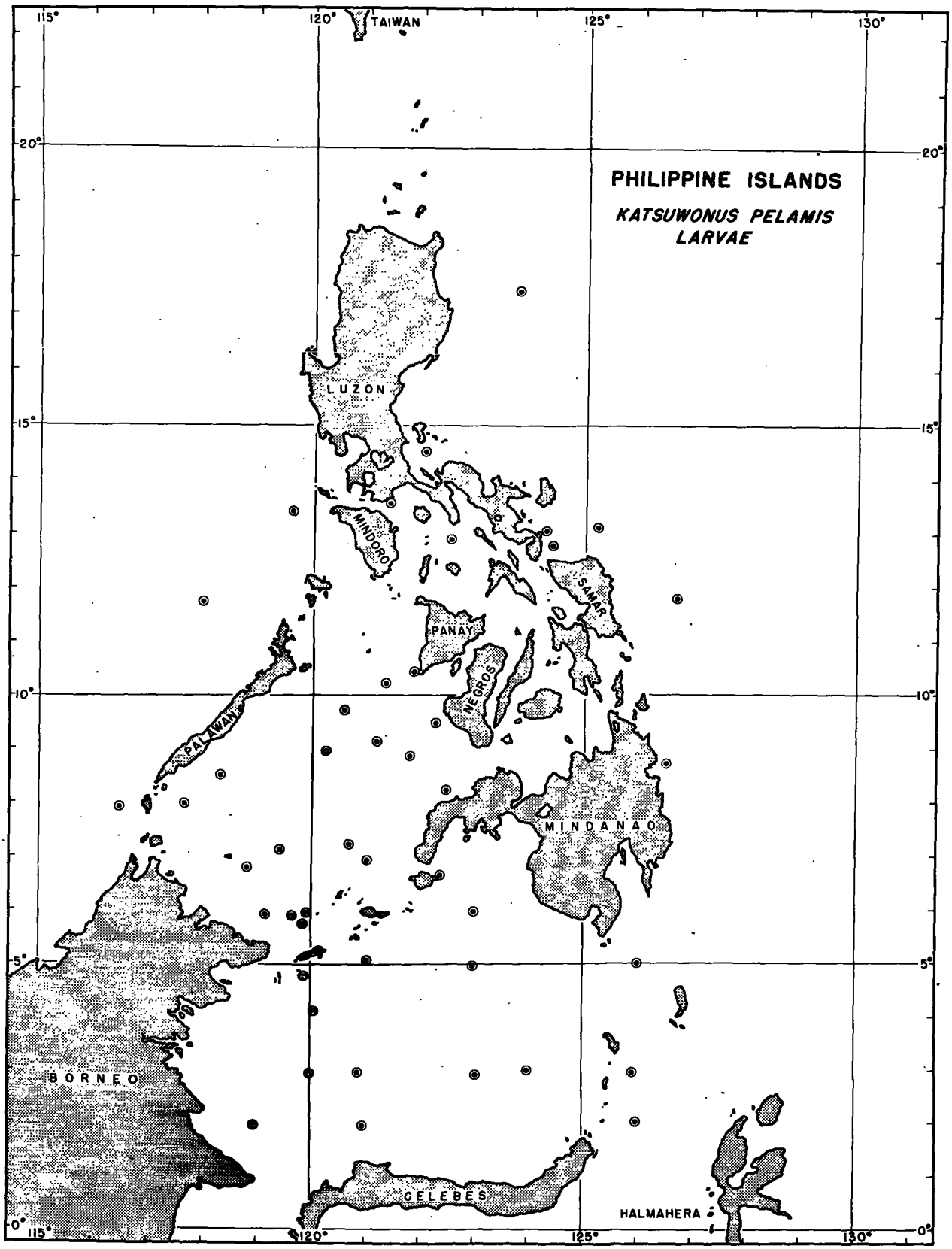

PHILIPPINE ISLANDS
KATSUWONUS PELAMIS
LARVAE
TAIWAN
LUZON
MINDORO
PANAY
NEGROS
SAMAR
PALAWAN
MINDANAO
BORNEO
CELEBES
HALMAHERA
115°
120°
125°
130°
20°
15°
10°
5°
0°

TABLE 13.—*Hourly summary of larval* Katsuwonus pelamis *collected in Philippine waters, 1947–49*

Hour	Total number of plankton tows	Tows with larvae		Larvae	
		Number	Percent	Number	Average catch per tow
0600–0659	26	2	7.71	3	0.11
0700–0759	18	2	11.10	5	.28
0800–0859	19	1	5.27	1	.05
0900–0959	23	1	4.35	1	.04
1000–1059	15				
1100–1159	18				
1200–1259	22				
1300–1359	19				
1400–1459	21				
1500–1529	16	1	6.26	1	.06
1600–1659	31	2	6.45	4	.13
1700–1759	22				
1800–1859	16	2	15.50	3	.19
1900–1959	21	4	19.00	10	.47
2000–2059	16	1	6.26	9	.56
2100–2159	23	4	15.40	19	.83
2200–2259	21	2	9.50	20	.95
2300–2359	17	1	5.27	1	.06
0000–0059	18	4	22.20	9	.50
0100–0159	13	4	30.70	13	1.00
0200–0259	21	6	28.50	32	1.52
0300–0359	15	4	26.60	7	.47
0400–0459	13	1	7.70	2	.15
0500–0559	18	3	16.60	14	.78

EUTHYNNUS YAITO (Kishinouye)

Family KATSUWONIDAE

Genus *Euthynnus* Lütken

Euthynnus Lütken, ms. in Jordan and Gilbert, 1882, Syn. Fish North America, Bull. 16, U. S. Nat. Mus., p. 429.

Euthynnus yaito (Kishinouye)

The smallest recognizable specimen of *Euthynnus yaito* in the collections is 3.7 mm. total length (fig. 17). The specimen is long and slender, especially posterior to the anal opening, and the head is not large in relation to the remainder of the body. The greatest depth is at a point defined by a vertical line drawn through the center of the eye. The dorsal and ventral outlines taper gradually to the end of the urostyle. The abdominal sac is small, somewhat triangular in shape, and placed anteriorly. The anal opening is located well forward of the center of the horizontal axis of the body.

The snout is short, about two-thirds of the eye diameter in length. The nostrils are not evident. No teeth can be seen in the large, slightly oblique mouth. The end of the maxillary reaches to a vertical line drawn through the pupil of the rather large eye.

TABLE 14.—*Station list of larval* Euthynnus yaito *collected in Philippine waters, 1947–49*

Station	Date	Latitude	Longitude	Specimens	
				Number	Size (mm.)
B-32	13 Oct. 1947	9°49′ N.	119°22.5′ E.	1	8.2
B-35	do	9°44′ N.	120°38′ E.	4	4.9–6.0
B-37	14 Oct. 1947	8°32′ N.	121°48.5′ E.	1	5.4
B-47	3 Dec. 1947	9°03′ N.	118°58′ E.	3	5.2–7.2
B-58	7 Dec. 1947	8°00.5′ N.	117°40′ E.	45	4.9–9.0
B-64	10 Dec. 1947	6°48.5′ N.	118°51.5′ E.	1	(1)
B-101	23 Feb. 1948	7° N.	123°49′ E.	15	4–6.1
B-112	26 Feb. 1948	6°22′ N.	125°53′ E.	1	6.5
B-120	1 Mar. 1948	3° N.	125° E.	1	5.2
B-123	2 Mar. 1948	2° N.	126° E.	7	4.8–6.3
B-124	3 Mar. 1948	3° N.	126° E.	2	5–5.5
B-133	7 Mar. 1948	1°06.3′ N.	123°59′ E.	1	5.0
B-138	8 Mar. 1948	4° N.	123° E.	1	6.6
B-154	10 Apr. 1948	1°29′ N.	121° E.	3	4.9–5.8
B-156	do	2° N.	121° E.	5	5.2–6.5
B-178	17 Apr. 1948	5°05′ N.	121°04.5′ E.	9	5.5–9.1
B-309	14 July 1948	7°26.5′ N.	116°55′ E.	7	6–8.0
B-333	31 July 1948	4° N.	118°44′ E.	1	7.0
B-339	1 Aug. 1948	1° N.	119°08′ E.	18	4.2–6.5
B-345	3 Aug. 1948	4°05′ N.	120°59′ E.	1	8.8
B-353	5 Aug. 1948	3° N.	122° E.	16	5.2–7.7
B-379	5 Sept. 1948	5° N.	125° E.	11	4–7.9
B-396	10 Sept. 1948	2° N.	126° E.	2	(1)
B-400	12 Sept. 1948	4° N.	125° E.	1	5.1
B-403	do	3° N.	124° E.	1	5.1
B-407	13 Sept. 1948	1°13′ N.	123° E.	2	4–4.5
B-415	15 Sept. 1948	6° N.	123° E.	8	5–7.0
B-484	21 Jan. 1949	13°35′ N.	120°07′ E.	25	5–9.9
B-485	22 Jan. 1949	13°24′ N.	119°39′ E.	13	5–7.8
B-490	23 Jan. 1949	12°50′ N.	120°37′ E.	7	5.1–7.4
B-494	24 Jan. 1949	12°24′ N.	120°52.5′ E.	18	5.7–7.0
B-495	do	12°07′ N.	121°04.5′ E.	6	7.4–10.1
B-498	do	11°45.3′ N.	121°11.2′ E.	10	6–8.3
B-500	25 Jan. 1949	10°52.5′ N.	121°51.5′ E.	7	8.2–11.0
B-502	do	10°36′ N.	120°37′ E.	3	6.5–8.0
B-503	do	10°19′ N.	120°03′ E.	34	5–7.1
B-507	27 Jan. 1949	7°33′ N.	120°29′ E.	1	6.1
B-510	28 Jan. 1949	6°56′ N.	118°14′ E.	17	4.7–8.9
B-518	1 Feb. 1949	7°57′ N.	116°31′ E.	1	(1)
B-529	3 Feb. 1949	11°44′ N.	118° E.	298	4.5–10.0
B-532	14 Feb. 1949	13°47′ N.	120°35′ E.	2	6.8–7.0
B-533	do	13°35′ N.	120°32′ E.	10	7.6–10.0
B-536	15 Feb. 1949	13°35′ N.	121°25′ E.	19	4.5–6.5
B-540	do	12°37.5′ N.	121°32.5′ E.	302	6–8.1
B-543	16 Feb. 1949	12°17′ N.	121°30′ E.	24	4–5.5
B-544	do	12°06′ N.	121°40′ E.	8	4.9–9.5
B-552	17 Feb. 1949	10°39′ N.	123°42′ E.	4	5.3–9.1
B-553	do	10°40′ N.	123°32.5′ E.	12	6–7.9
B-554	18 Feb. 1949	9°46′ N.	123°14.8′ E.	1	9.6
B-684	22 May 1949	16°07.5′ N.	122° E.	1	5.0
B-691	24 May 1949	14°30′ N.	122°04′ E.	1	6.8
B-696	do	15°35′ N.	124°40′ E.	3	5.8–6.6
B-888	6 Aug. 1949	16°21′ N.	120°12′ E.	5	5.8–6.6
B-943	26 Aug. 1949	5°10′ N.	119°25′ E.	135	7.1–11.0
B-946	do	5°01.5′ N.	119°38′ E.	10	7–9.9
B-948	do	6° N.	119°15′ E.	2	(1)
B-1003	5 Sept. 1949	10°27′ N.	121°51′ E.	2	5–6.0
B-1007	do	11°44′ N.	121°48′ E.	1	3.3
B-1114	19 Nov. 1949	11°56′ N.	123°19′ E.	7	5.9–6.2
B-1117	20 Nov. 1949	11°33′ N.	120°51′ E.	7	5–7.1

[1] Distorted.

There are three spines on the edge of the preoperculum. The center spine is the largest, flanked above by a slightly shorter and heavier spine, and below by a short blunt spine. The center spine extends obliquely downward and backward over the anterior part of the abdominal sac, while the upper spine extends slightly upward and backward. Two small spines can be seen on a slight crest on the surface of

FIGURE 16.—Localities in Philippine waters from which larval *Katsuwonus pelamis* were collected.

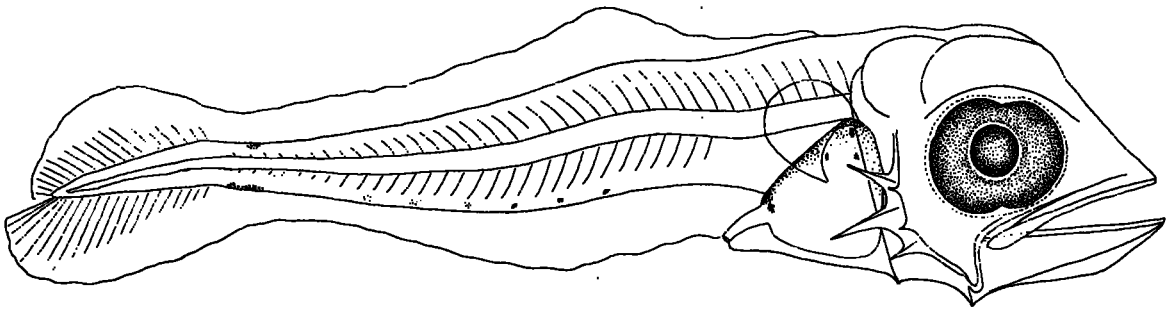


FIGURE 17.—*Euthynnus yaito*, 3.7 mm.

the preoperculum. The vertebrae cannot be distinguished, and the urostyle is long and slender.

Although the pectoral fin is present, the fin rays are not evident, and the ventral fins are absent. No median fins are present, but they are represented by a median-fin membrane extending backward along the dorsal midline from above the pectorals, around the posterior end of the body, and forward along the ventral midline to the anal opening. Although no fin rays are developed, faint vertical streaks can be seen in the membrane of the caudal region.

The body color is white in formalin-preserved specimens. No pigment is present on the head. The abdominal sac is pigmented dorsally and anteriorly with numerous, closely placed, small black chromatophores. An irregularly placed series of small black chromatophores, varying in number from two to seven, can be seen along the ventral midline in the region of the anal fin and caudal peduncle. Some specimens also possess several scattered black chromatophores along the posterior part of the dorsal midline.

A specimen 4.35 mm. in total length (fig. 18) very closely resembles the description of the preceding 3.7 mm. specimen.

Considerable development has taken place by the time this species reaches a total length of 6.5 mm. (fig. 19). The body is deeper and more robust, especially posteriorly. The head is larger and more pronounced in relation to the rest of the body, but the abdominal sac and the position of the anal opening have not changed to any extent.

The snout is long and pointed, its length slightly greater than the diameter of the eye. A large nostril can be seen on each side of the snout. The mouth is large, slightly oblique, and there are 9 to 10 teeth on each side of both jaws. The end of the maxillary reaches to a vertical drawn through the posterior margin of the pupil.

The edge of the preoperculum has seven spines: Two elongated slender spines at the angle (the lower and the longer is more slender), two small spines on the vertical edge, three along the horizontal edge. There are three small spines along a slight crest on

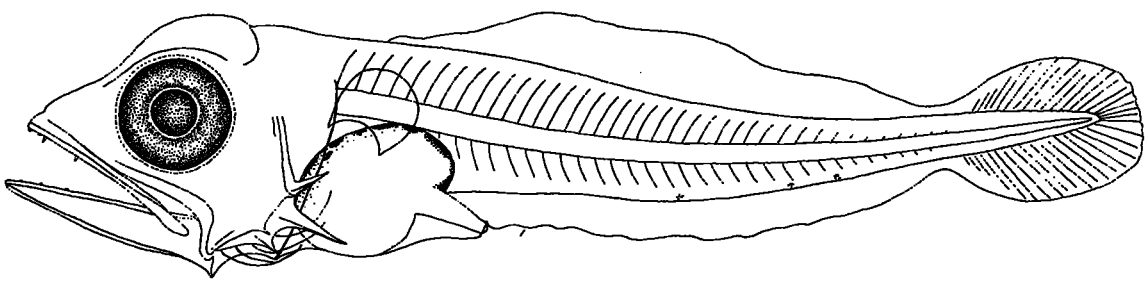


FIGURE 18.—*Euthynnus yaito*, 4.35 mm.

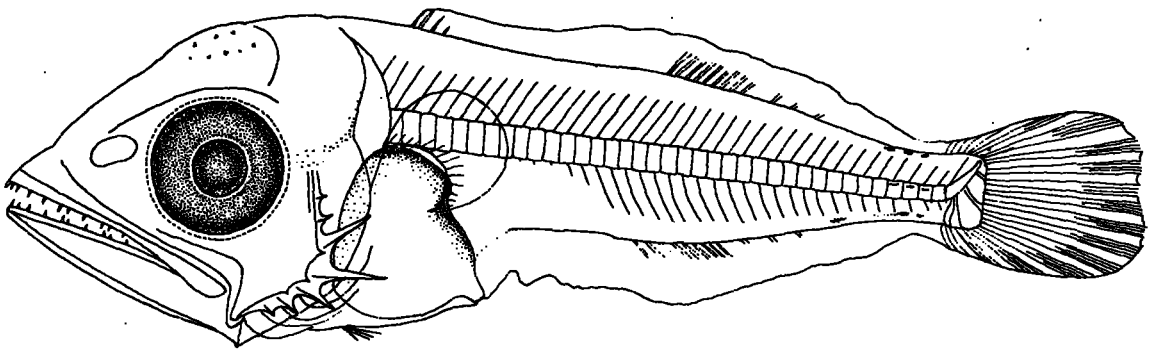


FIGURE 19.—*Euthynnus yaito*, 6.5 mm.

the surface of the preopercle. The vertebrae and the hypural plate can be faintly seen in cleared and stained specimens.

Both the pectoral and ventral fins are present but are largely undeveloped. Four small rays can be seen in the anterior portion of the first dorsal fin, while nine rays and three finlets can be traced faintly in both the second dorsal and the anal fins. The caudal fin is well developed, its posterior edge slightly concave.

The body color of formalin-preserved specimens is pale cream or white. A few scattered dark pigment spots are present on the membrane covering the brain and there is slight irregular pigmentation on the side of the head behind the eye. The peritoneum of the abdominal sac is densely pigmented dorsally with small black chromatophores. A faintly marked, irregular row of dark pigment lies along the posterior portion of the ventral midline. Several small chromatophores occur along the dorsal midline in the region of the caudal peduncle.

Only slight changes take place between 6.5 (fig. 19) and 7.5 mm. fork length (fig. 20) specimens. The body is more robust in the latter, and the head retains the same relative size as in the smaller specimen. The abdominal sac is slightly elongate, and the anal opening has moved more posteriorly. The snout is somewhat longer and more pointed. The single nostril on either side of the snout is beginning to constrict at its middle and to divide

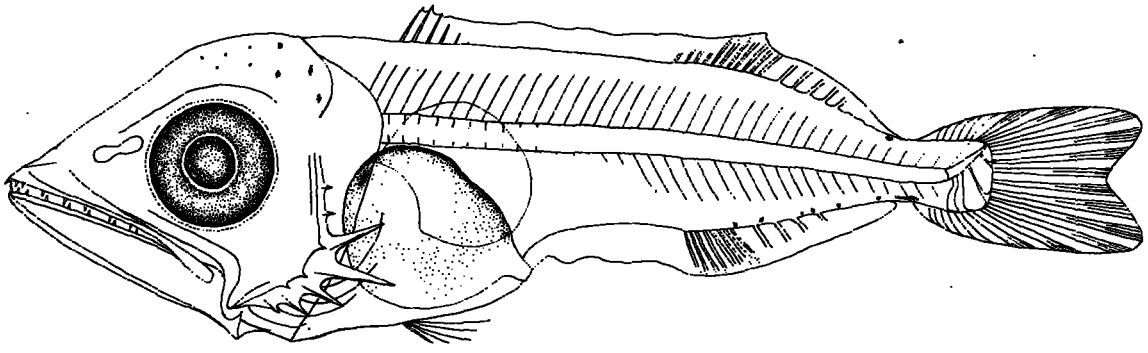


FIGURE 20.—*Euthynnus yaito*, 7.5 mm.

into two openings. The mouth and number of teeth in each jaw remain much the same.

There has been no change in the number of preopercular spines. The vertebrae in the 7.5 mm. specimen cannot be accurately distinguished, but the hypural plate is beginning to develop.

Poorly developed pectoral and ventral fins are present. Six short spines can be distinguished in the anterior portion of the first dorsal, and 11 rays and five finlets can be seen in the second dorsal fin. There are eight rays and four finlets in the anal fin. The caudal fin is well developed and slightly forked.

The color remains the same as in the smaller specimens except for the more heavily pigmented abdominal sac.

A specimen of 10.5 mm. fork length (fig. 21) closely resembles the juvenile form in general appearance. The body is heavy and robust, and the head large and well developed. The abdominal sac is becoming more elongated, and the anal opening is in a more posterior position, immediately anterior to the middle of the body.

The head of the 10.5 mm. specimen retains the same features as the 7.5 mm. specimen with the following exceptions: The single nostril on each side of the snout is becoming more constricted at its center and will shortly separate into an anterior and a posterior nasal opening; the number of teeth on each side of both jaws has increased from 11 to 13; 2 small temporal spines can be seen on each side of the nape; and both the vertebrae (total 39) and the hypural plate are well developed.

The first dorsal fin possesses 8 moderate-sized spines on the anterior portion. Nine rays and 8 finlets can be seen in the second dorsal, and 10 rays and 7 finlets in the anal fin. The caudal fin is well developed and slightly forked.

The general body color remains the same as in the small specimens, except that a heavier concentration of chromatophores appears on the membrane covering the brain, and a few scattered small spots of black pigment are present on the interradial membranes of the first dorsal fin.

Large specimens of larval *Euthynnus yaito*, approximately 9 to 10.5 mm. fork length, can be identified by the moderately developed first dorsal fin, which remains united with the second dorsal by a well-developed median fin-membrane. A short, irregular row of small black pigment spots is located along the base of the anal finlets and extends posteriorly to the caudal peduncle. A similar row of pigment spots usually is present along the base of the dorsal finlets and caudal peduncle. In both, the length and intensity of these pigmented rows vary considerably. The dorsal row may be reduced to one or two small chromatophores on the caudal peduncle, and occasionally they may be absent.

Quite similar at first glance to *Auxis* sp. (?), *Euthynnus yaito* larvae about 10 mm. long can be identified by the presence of the median membrane between the first and second dorsal fins, the larger, less posteriorly truncated head with a longer, more pointed snout, and a less obliquely placed mouth. The poorly developed first dorsal fin, smaller head, and body pigmentation separates *E. yaito* from *Katsuwonus pelamis*. The highly developed first dorsal fin, which is almost entirely dark, distinguishes specimens of *Neothunnus macropterus* from *E. yaito*.

From 6.5 to 8 mm. fork length, *Euthynnus yaito* is most easily confused with *Auxis* sp. (?), of all the

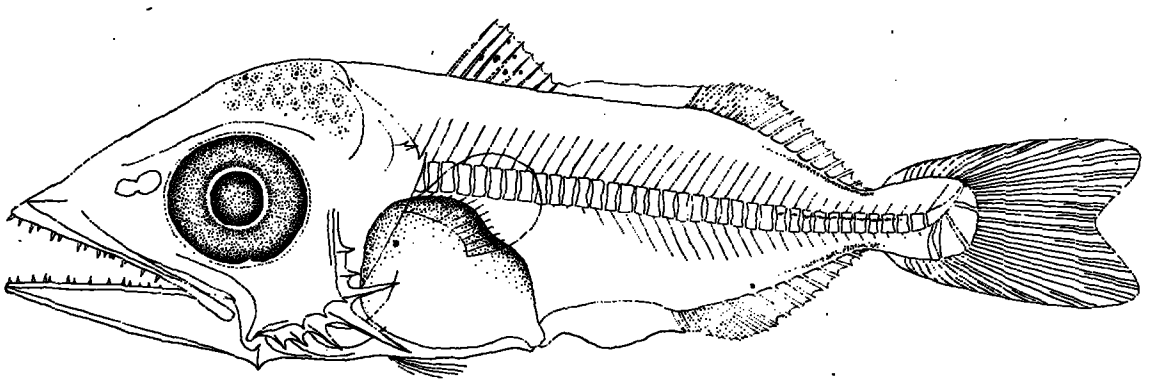


FIGURE 21.—*Euthynnus yaito*, 10.5 mm.

forms described in this bulletin. However, in *E. yaito* several of the rays of the first dorsal fin are present, even in the smaller specimens, while they are absent in *Auxis* sp. (?). The median fin membrane is much more highly developed in *E. yaito*, while it is reduced to a very narrow band in *Auxis* sp. (?) and is sometimes almost entirely absent. Also the head is larger, less truncated posteriorly, and the snout is longer and more pointed. The row of pigment along the posterior portion of the dorsal and ventral midline is present in some degree in both *Auxis* sp. (?) and *E. yaito*, but it seems to be more greatly developed in the former.

Specimens of *Katsuwonus pelamis* can be separated from *Euthynnus yaito* by the larger head, the lack of body pigmentation, and a more highly elevated first dorsal fin among the larger specimens. A highly developed first dorsal fin also distinguishes *Neothunnus macropterus* from *E. yaito* in 6.5 to 8 mm. specimens.

Specimens of *Euthynnus yaito* of 5 mm. or less in length are quite difficult to separate from *Auxis* sp. (?). No median fins are developed in either species, but the median fin membrane of *E. yaito* is much more highly developed than in *Auxis* sp. (?). Although the preopercular spines usually were not considered a good identification character it was found that in *E. yaito* of 5 mm., only three spines have developed on the preopercular edge, while on *Auxis* sp. (?) five spines were formed.

The pigmentation on the head and abdominal sac of *Euthynnus yaito* differs somewhat from *Auxis* sp. (?). In *E. yaito* ordinarily there are no pigment spots in the area over the brain, and the pigment spots of the abdominal sac are numerous and dark. The pigmentation on the head of most specimens of *Auxis* sp. (?) is composed of a few small scattered areas of dark chromatophores, although this configuration varies considerably and may be absent in some specimens. On the abdominal sac of *Auxis* sp. (?) the dark pigmentation is often arranged in a few small scattered areas.

The head is more truncated posteriorly in *Auxis* sp. (?) and the eye is smaller than in *E. yaito*. The development of the abdominal sac seems to be more advanced in *Euthynnus yaito*, but this feature needs to be examined more thoroughly in a larger series of specimens.

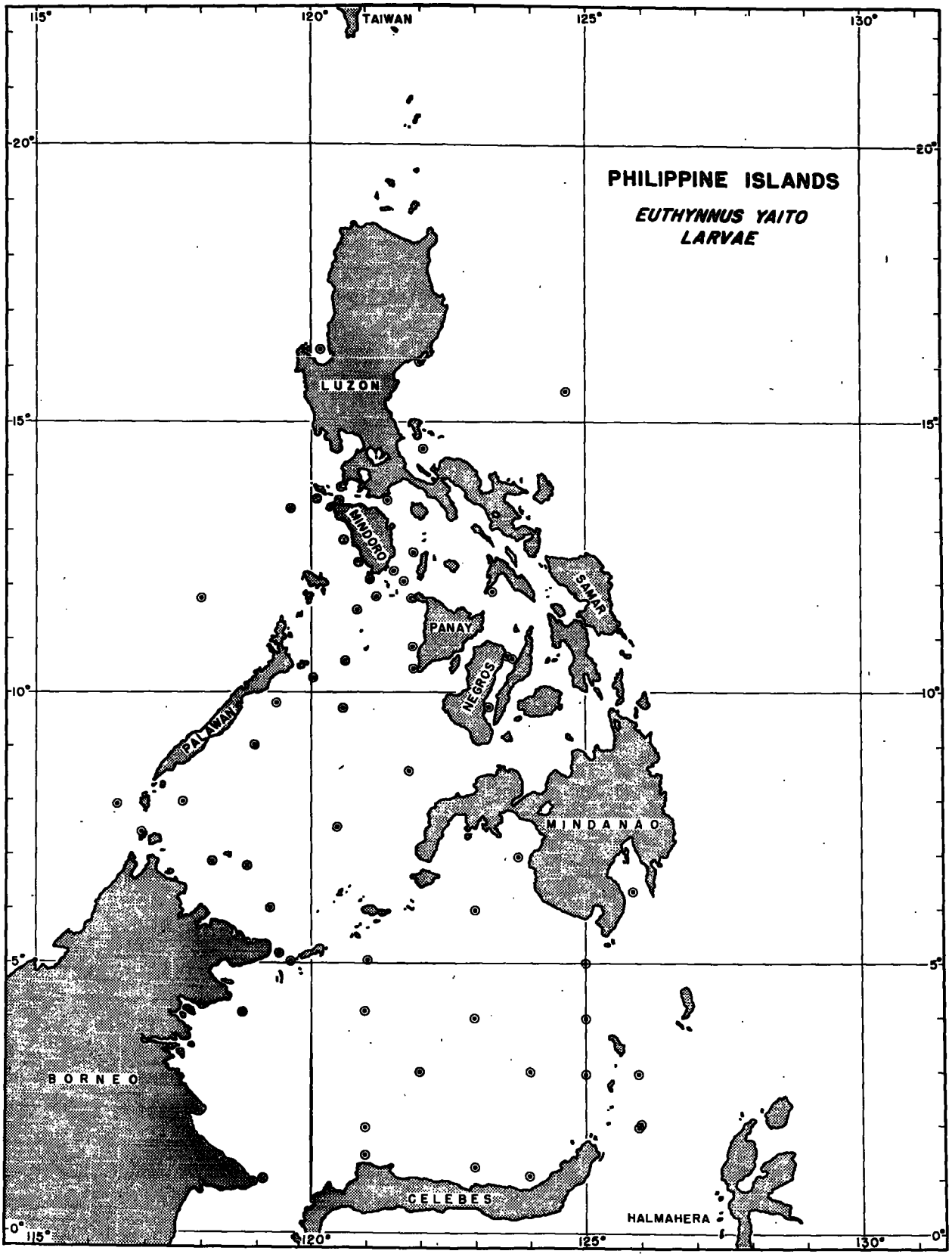
Although the larvae of *Euthynnus yaito* were collected throughout most of the year, they occurred most abundantly from November through April. No specimens were taken during June, and net tows in May, July, and October did not produce larvae in any abundance. A small increase was noted during August and September in the number of larvae collected.

TABLE 15.—*Monthly catch of larval* Euthynnus yaito *taken in Philippine waters, 1947–49*

Month	Total number of plankton tows	Tows with larvae		Larvae	
		Number	Percent	Number	Average catch per tow
1947					
October	21	3	14.2	6	0.28
December	15	3	20.0	49	3.27
1948					
February	10	2	20.0	16	1.60
March	18	5	27.8	12	.67
April	27	3	11.1	17	.63
June	27				
July	25	2	8.0	8	.32
August	17	3	17.6	35	2.06
September	28	6	21.4	25	.89
1949					
January	30	11	36.7	141	4.70
February	43	11	25.6	681	15.70
May	38	3	7.9	5	.13
June	25				
July	18				
August	50	4	8.0	152	3.40
September	35	2	5.7	3	.09
October	20				
November	16	2	12.5	14	.87
All	463	60	13.0	1,164	2.51

Based upon present collections, it appears that the spawning activities of *Euthynnus yaito* take place throughout the year and occur most intensively during the winter and spring months. Spawning seems to be reduced to a minimum during the summer months, except for August, when a slight increase was noted. As in the other species previously discussed, it should be remembered that the data may not present a true picture of the abundance of larvae throughout the entire area. It is entirely possible that at the time the research vessel was working in unproductive areas, larvae in other areas of Philippine waters may have been abundant.

There were considerable differences in the number of *Euthynnus yaito* larvae collected and in the number of successful tows made between the day and night operations. A total of 250 hauls were made during the daylight hours of 0600 to 1800. Sixteen tows (6.4 percent) were successful in capturing 97 larvae with an average of 0.39 specimen for all tows. During the night, 212 hauls were made, and 43 (20.2 percent) were successful. A total of 1,070 specimens were captured during the night operations for an average of 5.05 specimens for all tows. *E. yaito*, like


PHILIPPINE ISLANDS
EUTHYNNUS YAITO
LARVAE
TAIWAN
LUZON
MINDORO
SAMAR
PANAY
NEGROS
PALAWAN
MINDANAO
BORNEO
CELEBES
HALMAHERA
115°
120°
125°
130°
20°
15°
10°
5°
0°

Katsuwonus pelamis, migrates to beneath the surface during the day and returns to the surface at night.

TABLE 16.—*Hourly summary of larval* Euthynnus yaito *collected in Philippine waters, 1947–49*

Hour	Total number of plankton tows	Tows with larvae		Larvae	
		Number	Percent	Number	Average catch per tow
0600–0659	26	2	7.7	13	0.50
0700–0759	18	1	5.5	7	.39
0800–0859	19	2	10.5	11	.58
0900–0959	23	1	4.4	2	.09
1000–1059	15	1	6.8	24	1.60
1100–1159	18				
1200–1259	22				
1300–1359	19	1	5.3	8	.42
1400–1459	21	3	14.3	13	.62
1500–1559	16	1	6.2	1	.06
1600–1659	31	2	6.5	5	.16
1700–1759	22	2	9.1	13	.59
1800–1859	16	3	18.7	9	.56
1900–1959	21	7	33.3	619	29.50
2000–2059	16	2	12.5	49	3.06
2100–2159	23	4	17.4	55	2.38
2200–2259	21	2	9.5	9	.43
2300–2359	17		7.0		
0000–0059	18	4	22.2	25	1.39
0100–0159	13	5	38.4	14	1.07
0200–0259	21	6	28.5	67	3.19
0300–0359	15	5	33.3	56	3.73
0400–0459	13	3	23.0	3	.23
0500–0559	18	2	22.2	164	9.12

AUXIS SP.(?)

Family KATSUWONIDAE

Genus *Auxis* Cuvier

Auxis Cuvier, 1829, Règne Animal, ed. II, vol. 2, p. 199, type *Scomber rochei* Risso = *Scomber thazard* Lacépède.

Auxis sp. (?)

Two species of the genus *Auxis* occur in Philippine waters (Wade, 1949), but the present collections have provided insufficient data to differentiate between the larvae of the two forms.

The smallest specimen that can be assigned to this genus is 5.1 mm. total length (fig. 23). The body is very slender and elongate, especially in the postanal region. The head is of moderate size and quite short. The abdominal sac protrudes ventrally below the body outline and is placed anteriorly. The anal opening is far cephalad of the middle of the body.

The snout is short and sharply pointed with its dorsal and ventral outlines equally and steeply sloped. The dorsal outline of the head is somewhat bulged over the brain. The eye is large, and its diameter is equal to or greater than the length of the snout. The tip of the snout is at about mid-depth of the head. The mouth is sharply oblique, and the end of the maxillary reaches to a vertical drawn through the center of the pupil. There are from three to five small pointed teeth on each side of both jaws. The lower jaw is slightly included at the tip. The nostrils are not visible.

TABLE 17.—*Station list of larval specimens of* Auxis *sp.* (?) *collected in Philippine waters, 1947–49*

Station	Date	Latitude	Longitude	Specimens	
				Number	Size (mm.)
B–124	3 Mar. 1948	3° N.	126° E.	6	5.8–6.8
B–156	10 Apr. 1948	2° N.	121° E.	1	5.8
B–177	16 Apr. 1948	5° N.	120°30′ E.	1	(1)
B–187	20 Apr. 1948	7° N.	123° E.	1	5.1
B–188	20 Apr. 1948	6°57′ N.	122°25′ E.	1	5.9
B–339	1 Aug. 1948	1° N.	119°08′ E.	2	4.2–4.3
B–486	22 Jan. 1949	12°42.5′ N.	119°32.5′ E.	2	(1)
B–492	23 Jan. 1949	12°32.5′ N.	120°08.5′ E.	1	7.3
B–495	24 Jan. 1949	12°07′ N.	121°04.5′ E.	95	5–11.6
B–497	do	11°31′ N.	120°39′ E.	2	4.6–6.8
B–499	do	11°43′ N.	121°48′ E.	3	(1)
B–501	25 Jan. 1949	10°56′ N.	120°52.5′ E.	3	5.6–5.8
B–502	do	10°36′ N.	120°37′ E.	10	6.1–9.1
B–515	31 Jan. 1949	7°40.5′ N.	117° E.	1	6.1
B–529	3 Feb. 1949	11°44′ N.	118° E.	3	5–8.2
B–551	17 Feb. 1949	11°04′ N.	123°48′ E.	1	6.2
B–574	23 Feb. 1949	12°37′ N.	123°27.3′ E.	1	5.2
B–577	24 Feb. 1949	12°51′ N.	122°47′ E.	1	5.1
B–819	18 July 1949	7°12′ N.	116°12′ E.	1	11.0
B–832	19 July 1949	10°25′ N.	117°46′ E.	4	5–5.8
B–1118	21 Nov. 1949	10°45′ N.	120°40′ E.	3	5.8–7

[1] Distorted.

Five spines are present along the edge of the preoperculum: Two large slender spines at the angle, one small spine on the vertical edge, and two small spines on the horizontal edge. Three small spines are present on a slight crest lying on the surface of the preoperculum. The vertebrae cannot be distinguished at this size in cleared and stained specimens. The urostyle is long and slender and bent slightly upward at the tip.

The pectoral fins are represented by small rounded, poorly developed membranes covering the anterior portion of the abdominal sac, but the ventral fins are absent. Median fins are not present, but they are represented by a continuous median fin membrane extending backward along the dorsal midline from immediately posterior to the pectoral base, around the end of the tail, and forward along the ventral midline almost to the anal opening. Faint vertical striations are visible in the region of the caudal fin.

The body color of formalin-preserved specimens is white. A few small spots of black pigment are scat-

FIGURE 22.—Localities in Philippine waters from which the larvae of *Euthynnus yaito* were collected.

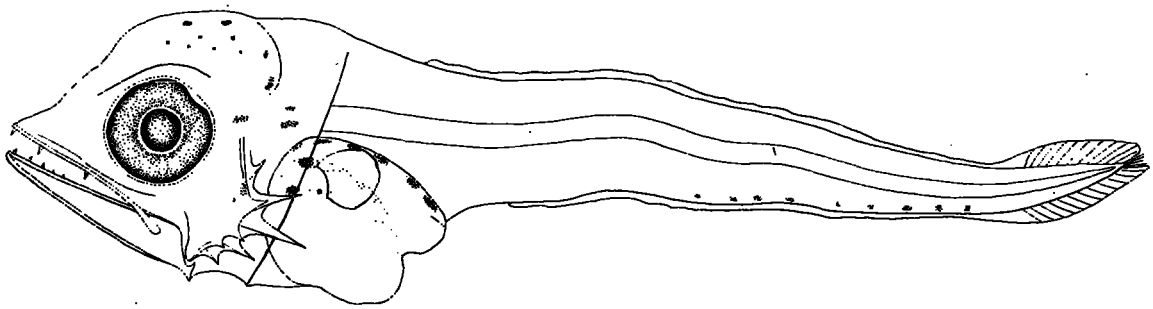


FIGURE 23.—*Auxis* sp. (?), 5.1 mm.

tered over the membrane covering the brain. Several small, faintly marked pigment areas are distributed on the sides of the head posterior to the eye. The peritoneal lining of the abdominal sac has a few, scattered oval areas of black pigment. A series of small black-pigmented areas extends anteriorly along the ventral midline from the region of the caudal peduncle almost to the midpoint of the body.

Only slight changes have taken place in *Auxis* sp. (?) by the time it has reached 6.8 mm. total length (fig. 24). The body has become deeper and heavier. The head is not excessively large in relation to the body and remains truncated posteriorly.

The edge of the preoperculum bears seven spines: Two long slender spines at the angle, two small spines on the vertical edge, and three small spines on the horizontal edge. The vertebrae remain undeveloped. The nostrils are not visible.

The caudal fin is well developed, but the other median fins remain undeveloped. The median fin membrane has become partly degenerate in the region of the caudal peduncle. The pectoral fins remain small and undeveloped, and the ventral fins are represented by minute "buds."

The body color of formalin-preserved specimens is white. The color markings remain the same as in the 5.1-mm. specimen, except that the peritoneum lining the abdominal sac is more heavily marked, and a slight dark pigmentation occurs at the dorsal midline of the caudal peduncle in some specimens.

Several changes have occurred by the time specimens have reached 9.7 mm. fork length (fig. 25). The body remains slender and elongated. The dorsal outline of the body, from the nape to the origin of the second dorsal fin, is flat or slightly concave. The head is large, truncated posteriorly, and the dorsal outline is expanded above the brain. The abdominal sac is becoming somewhat elongated, and the anal opening is moving posteriorly toward the middle of the body.

The wedge-shaped snout is short and pointed, and the slopes of the dorsal and ventral outlines are almost equal. The diameter of the eye is equal to or slightly greater than the snout length. The mouth is oblique, and the tip of the maxillary is at the mid-

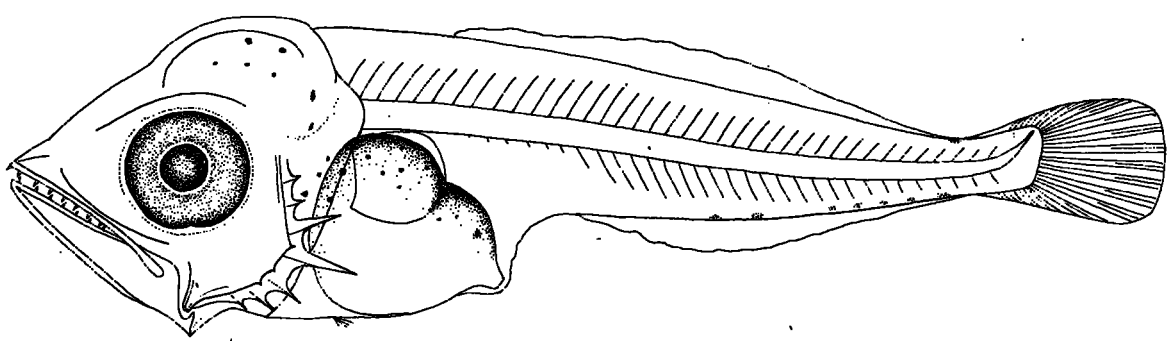


FIGURE 24.—*Auxis* sp. (?), 6.8 mm.

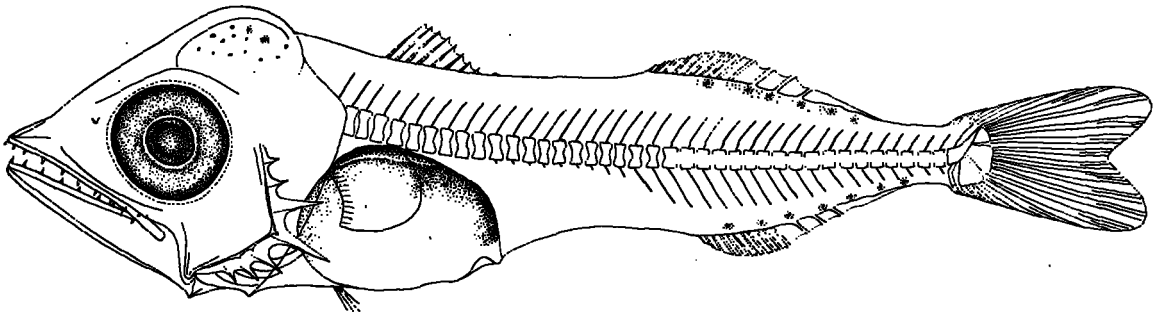


FIGURE 25.—*Auxis* sp. (?), 9.7 mm.

depth of the head. There are 8 to 10 teeth on each side of both jaws The end of the maxillary reaches to a vertical drawn through the posterior edge of the pupil.

The number and position of the preopercular spines remain the same as in the 6.8 mm. specimen. Anteriorly, the vertebrae can be easily seen, but are only faintly discernible posteriorly. The hypural plate is well developed.

The dorsal fin has 9 rays and is separated by a long interspace from the second dorsal, which has 10 rays. The anal fin has 11 rays. Three dorsal and anal finlets can be seen faintly. The median fin-membrane has completely disappeared from the interspace between the two dorsal fins and from the dorsal and ventral midlines of the caudal peduncle. The caudal fin is well developed and slightly forked. The pectoral and ventral fins are present and moderately developed.

The body color of preserved specimens remains white. A few small scattered black-pigmented areas are found on the membrane covering the brain. The abdominal sac is heavily pigmented dorsally with small chromatophores. The posterior portions of the dorsal and ventral midlines are faintly pigmented with an irregular row of small dark spots.

An 11.6 mm. fork-length specimen (fig. 26) is almost identical with the 9.7 mm. specimen. Its general appearance is quite similar to the smaller juvenile forms. There are from 11 to 13 teeth on each side of both jaws. The preopercular spines remain the same. The first dorsal fin, with 13 developed spines, is widely separated from the second dorsal fin which has 16 rays and 7 finlets. There are 18 plus 21 well-developed vertebrae. Only one nostril opening is evident on each side of the snout. The color pattern remains the same as in the 9.7 mm. specimen.

The only other species of larval tuna described in this bulletin with which *Auxis* sp. (?) is likely to be confused is *Euthynnus yaito*. Specimens of *Auxis* sp. (?) larger than 9 mm. fork length can be identified easily by the widely separated dorsal fins which are without a connecting median fin-membrane. The head is of moderate size, truncated posteriorly,

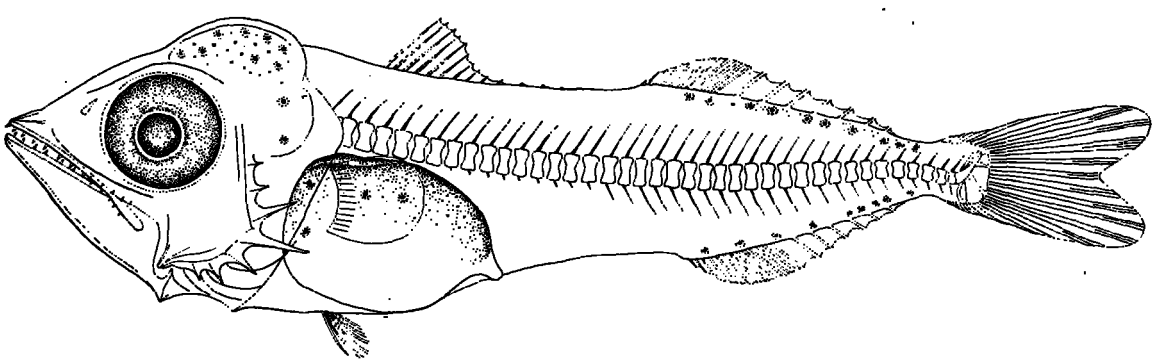
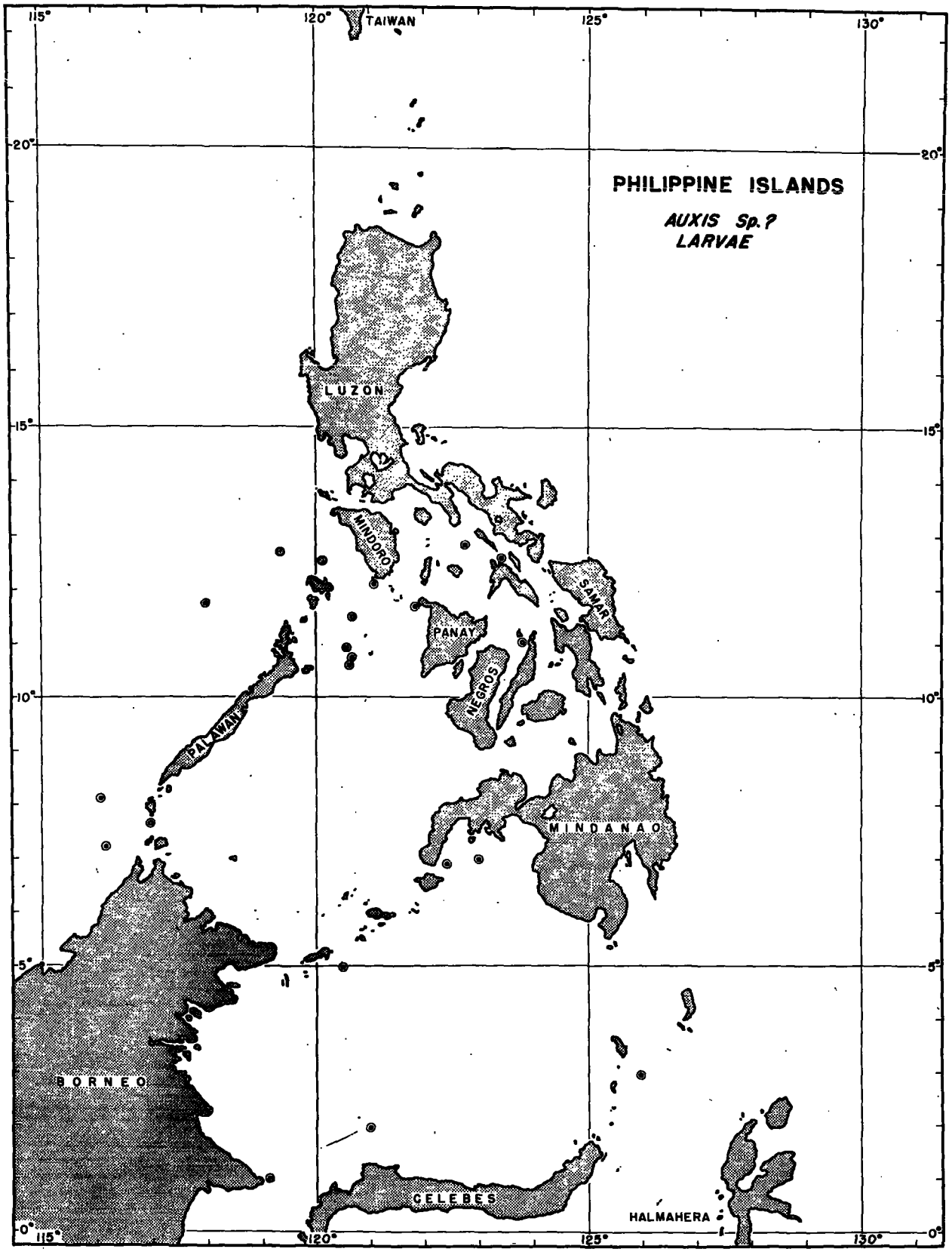


FIGURE 26.—*Auxis* sp. (?), 11.6 mm.


PHILIPPINE ISLANDS
AUXIS Sp.?
LARVAE
TAIWAN
LUZON
MINDORO
PANAY
NEGROS
SAMAR
PALAWAN
MINDANAO
BORNEO
CELEBES
HALMAHERA
115°
120°
125°
130°
20°
15°
10°
5°
0°

while the snout is short and bluntly wedge-shaped. The mouth is oblique, and the tip of the maxillary lies at about mid-depth of the head.

Medium-sized specimens of *Auxis* sp. (?) from 5 to 9 mm. can be distinguished from *Euthynnus yaito* by the more poorly developed median fin-membrane. The later development and slower growth of the first dorsal rays and the characteristic features of the head of *Auxis* sp. (?) have already been discussed. The row of pigment along the posterior portion of the ventral midline is similar in both forms, but it seems to extend more anteriorly on most specimens of *Auxis* sp. (?). The large head and the almost entire lack of body pigment separates *Katsuwonus pelamis* from *Auxis* sp. (?), whereas the large highly developed first dorsal and lack of body pigment defines *Neothunnus macropterus*.

Small examples of *Auxis* sp. (?) are difficult to distinguish from larval *Euthynnus yaito*. The less well-developed median fin-membrane, the short, truncated head, the short, bluntly pointed snout, and a greater number of preopercular spines usually will identify *Auxis* sp. (?). Damaged specimens, or those in which the features are distorted, are often impossible to identify. In *Neothunnus macropterus* of 5 to 9 mm., the head is larger, and no body pigment is present. *Katsuwonus pelamis* is distinguished by the large head, long snout, wide gape, and absence of a row of pigment spots posteriorly along the ventral midline.

The greatest catch of *Auxis* sp. (?) larvae was made during January, February, and March. The collection during the remainder of the year was meager, and these data coincide with those obtained during a study of the public fish market of Batangas, Luzon. Small juvenile *Auxis* sp. (?) begin to appear on the market in late November and are found in increasing numbers until January and February, when they begin to decrease in quantity, and are not found after May. These marketed juveniles were caught in both Batangas and Balayan Bays which are well sheltered. They were captured in fish traps and several types of local nets, both close to the shore and in open water. It is believed that for spawning *Auxis* sp (?) usually prefers protected, more or less shallow areas, fairly close to land. As the research work of the Philippine Fishery Program was conducted primarily on the high seas, and only occasionally in protected waters, it is possible that the collections do not represent the normal distribution and relative abundance of

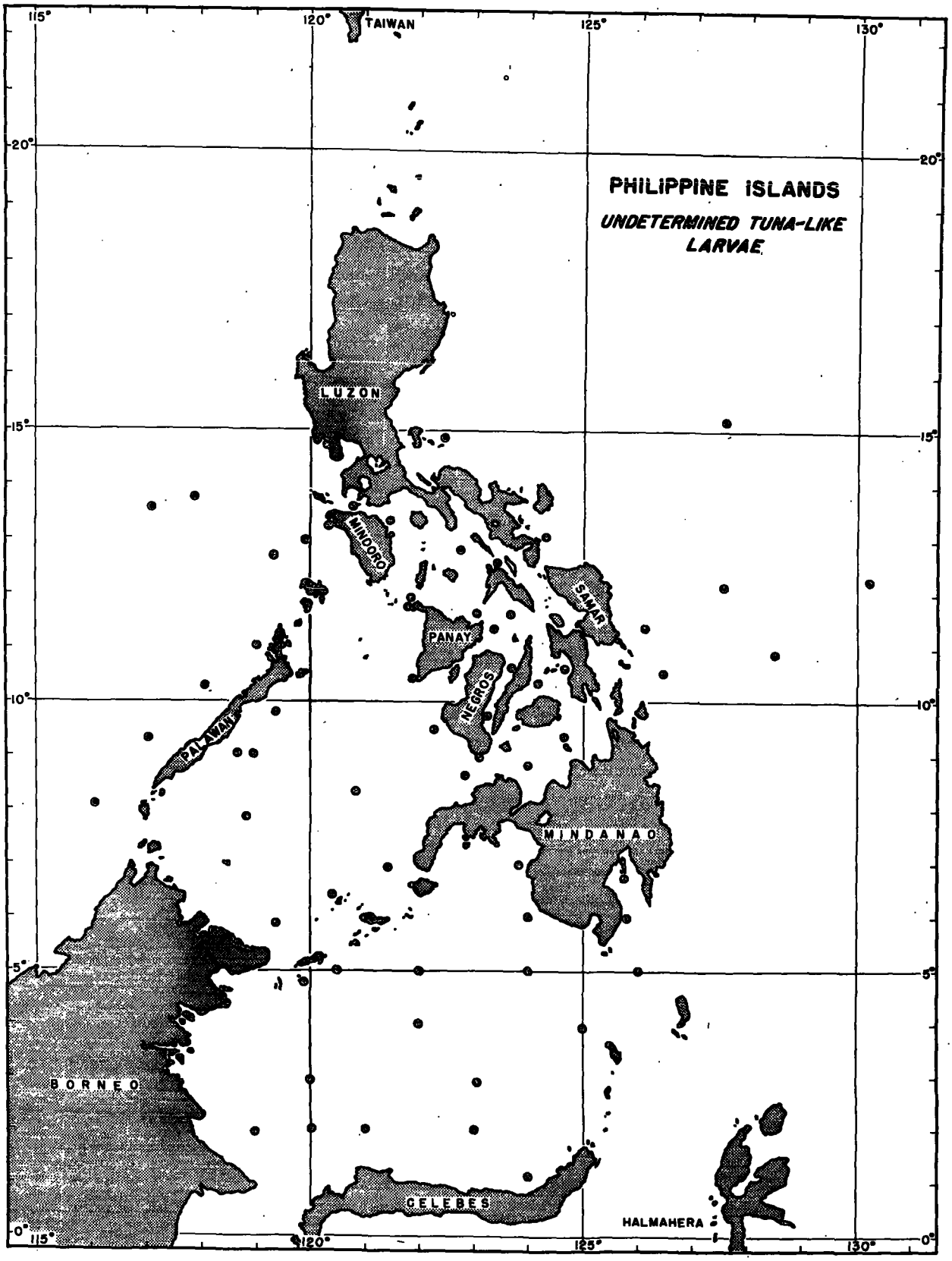
TABLE 18.—*Monthly catch of larval* Auxis *sp.* (?) *taken in Philippine waters, 1947–49*

Month	Total number of plankton tows	Tows with larvae		Larvae	
		Number	Percent	Number	Average catch per tow
1947					
October	21				
December	15				
1948					
February	10				
March	18	1	5.5	6	0.33
April	27	4	14.8	4	.15
June	27				
July	25				
August	17	1	5.9	2	.12
September	28				
1949					
January	30	8	26.8	117	3.9
February	43	4	9.3	6	.14
May	38				
June	25				
July	18	2	11.1	5	.28
August	50				
September	35				
October	20				
November	16	1	6.3	3	.19
All	463	21	4.5	143	0.31

TABLE 19.—*Hourly summary of larval* Auxis *sp.* (?) *collected in Philippine waters, 1947–49*

Hour	Total number of plankton tows	Tows with larvae		Larvae	
		Number	Percent	Number	Average catch per tow
0600–0659	26	2	7.6	96	3.70
0700–0759	18	2	11.1	4	.22
0800–0859	19	2	10.5	3	.16
0900–0959	23				
1000–1059	15				
1100–1159	18				
1200–1259	22	2	9.1	2	.09
1300–1359	19	3	15.8	3	.16
1400–1459	21				
1500–1559	16				
1600–1659	31	2	6.4	11	.35
1700–1759	22	1	4.5	4	.18
1800–1859	16	2	12.5	2	.13
1900–1959	21	1	4.8	3	.14
2000–2059	16				
2100–2159	23				
2200–2259	21	1	4.8	1	.05
2300–2359	17	2	11.7	4	.23
0000–0059	18				
0100–0159	13				
0200–0259	21	2	9.5	3	.14
0300–0359	15	1	6.7	6	.40
0400–0459	13				
0500–0559	18	1	5.5	1	.05

FIGURE 27.—Localities in Philippine waters from which the larvae of *Auxis* sp. (?) were collected.


PHILIPPINE ISLANDS
UNDETERMINED TUNA-LIKE LARVAE
TAIWAN
LUZON
MINDORO
PANAY
NEGROS
SAMAR
PALAWAN
MINDANAO
BORNEO
CELEBES
HALMAHERA
115°
120°
125°
130°
20°
15°
10°
5°
0°

this genus. From the collections and data secured from the public market, it appears that the principal spawning activities occur during the winter and that scattered spawning takes place the remainder of the year.

A 4 mm. specimen was assigned tentatively to the genus *Auxis* sp. (?) by Kishinouye (1926). It was captured in a plankton net off Takarajima, Japan, 29°09′ N., 129°13′ E., June 8, 1924. Although the illustration is not available for study, the brief description more closely approaches that of *Euthynnus yaito* than of *Auxis* sp. (?) and, as observed by Kishinouye, it may actually have been *E. yaito*.

The hourly catches are too meager to determine the differences, if any, between the abundance of material in day and night tows. A large sample taken at 0600 to 0630 hours has distorted the true picture of the average daytime catches, although the percentage of successful tows is slightly greater during the day than at night. Only 14 of 250 tows (5.6 percent) were successful during the day; 9 of 212 tows (4.3 percent) were successful at night. Ignoring the single large sample, the average catch of both day and night tows is about the same: An average of 0.11 specimen during the day and 0.09 during the night. The rather inadequate data indicate that the diurnal and nocturnal abundance of larval *Auxis* sp. (?) at the surface is approximately the same.

UNDETERMINED TUNA-LIKE LARVAE

It was impossible to identify a portion of the collection of tuna-like larvae, particularly smaller specimens which were badly damaged or distorted. Beyond the fact that they were tuna-like, nothing could be specifically determined. Neither was it possible at times to identify small isolated specimens which did not possess characters sufficiently well developed to determine their proper taxonomic status. A list of those stations at which undetermined larvae were found is given in table 20 and plotted on figure 28.

TABLE 20.—*Station list of unidentified tuna-like larvae collected in Philippine waters, 1947–49*

Station	Date	Latitude	Longitude	Specimens	
				Number	Size (mm.)
B-22	9 Oct. 1947	8°41′ N.	122°50′ E.	1	4.5
B-32	13 Oct. 1947	9°49′ N.	119°22.5′ E.	1	4.5
B-47	3 Dec. 1947	9°03′ N.	118°58′ E.	6	(1)
B-56	6 Dec. 1947	7°54′ N.	118°51′ E.	7	(2)
B-127	3 Mar. 1948	4° N.	125° E.	1	(2)
B-160	12 Apr. 1948	3° N.	120° E.	1	(2)
B-244	16 June 1948	10°45′ N.	121°48′ E.	1	(2)
B-258	19 June 1948	6°48′ N.	121°26′ E.	1	(2)
B-261	20 June 1948	8°20′ N.	120°50′ E.	1	(2)
B-294	10 July 1948	6°26.5′ N.	120°24′ E.	1	5.0
B. 296	11 July 1948	5°53′ N.	119°23′ E.	1	(2)
B-329	30 July 1948	5° N.	120°30′ E.	1	(2)
B-330	do	4°45′ N.	119°53′ E.	2	(2)
B-338	1 Aug. 1948	1°56.5′ N.	119° E.	1	(2)
B-342	2 Aug. 1948	2° N.	120° E.	1	(2)
B-348	4 Aug. 1948	2° N.	121° E.	15	(2)
B-355	6 Aug. 1948	4° N.	122° E.	1	4.1
B-356	6 Aug. 1948	5° N.	122° E.	6	(2)
B-375	4 Sept. 1948	7° N.	123°49′ E.	3	(2)
B-376	5 Sept. 1948	6° N.	124° E.	1	4.8
B-378	do	5° N.	124° E.	1	5.8
B-383	6 Sept. 1948	5° N.	126° E.	1	4.7

See footnotes at end of table.

TABLE 20.—*Station list of unidentified tuna-like larvae collected in Philippine waters, 1947–49*—Continued

Station	Date	Latitude	Longitude	Specimens	
				Number	Size (mm.)
B-384	7 Sept. 1948	6° N.	125°48′ E.	2	(2)
B-388	do	6°44′ N.	125°46′ E.	2	(2)
B-405	13 Sept. 1948	1°08′ N.	124° E.	2	(2)
B-408	14 Sept. 1948	2° N.	123° E.	1	(2)
B-411	do	2°56′ N.	123°03.5′ E.	2	(2)
B-482	14 Jan. 1949	14°30′ N.	119°50′ E.	1	5.0
B-486	22 Jan. 1949	12°42.5′ N.	119°32.5′ E.	2	5.5–6.0
B-487	do	12°59′ N.	119°56′ E.	1	6.0
B-488	do	13°16′ N.	120°21′ E.	4	(2)
B-523	2 Feb. 1949	10°17′ N.	118°06′ E.	1	3.8
B-527	3 Feb. 1949	11°03′ N.	119°03′ E.	5	(2)
B-534	14 Feb. 1949	13°37′ N.	120°47′ E.	9	(2)
B-535	15 Feb. 1949	13°22′ N.	121°27′ E.	2	(2)
B-545	16 Feb. 1949	11°55′ N.	121°50′ E.	4	(2)
B-552	17 Feb. 1949	10°39′ N.	123°42′ E.	10	(2)
B-554	18 Feb. 1949	9°46′ N.	123°14.8′ E.	2	(2)
B-559	19 Feb. 1949	10°23′ N.	124°09′ E.	2	4.7–5.0
B-560	do	10°40′ N.	124°38′ E.	5	4.2–4.6
B-574	23 Feb. 1949	12°37′ N.	123°27.3′ E.	1	6.0
B-577	24 Feb. 1949	12°51′ N.	122°47′ E.	1	5.8
B-661	18 May 1949	21°19′ N.	123°31′ E.	2	(2)
B-680	21 May 1949	17°06.5′ N.	122°36.7′ E.	1	(2)
B-695	24 May 1949	14°52′ N.	122°28.9′ E.	4	(2)
B-718	27 May 1949	15°12′ N.	127°36′ E.	2	(2)
B-730	29 May 1949	12°10′ N.	127°35′ E.	1	(2)
B-823	18 July 1949	8°07.5′ N.	116°07′ E.	1	4.0
B-825	19 July 1949	9°20′ N.	117°03.5′ E.	2	(2)
B-864	1 Aug. 1949	13°45′ N.	117°53′ E.	6	(2)
B-866	do	13°34′ N.	117°07′ E.	2	5.0–5.3
B-967	29 Aug. 1949	9°04′ N.	118°40′ E.	1	4.9
B-996	4 Sept. 1949	9° N.	123°03′ E.	1	(2)
B-1000	5 Sept. 1949	9°31′ N.	122°15′ E.	2	(2)
B-1003	do	10°27′ N.	121°51′ E.	2	(2)
B-1034	15 Sept. 1949	13°07′ N.	124°18′ E.	1	(2)
B-1042	19 Sept. 1949	9° N.	124°39′ E.	1	(2)
B-1046	20 Sept. 1949	8°50′ N.	123°57′ E.	1	(2)
B-1076	17 Oct. 1949	11°25′ N.	126°07′ E.	1	(2)
B-1077	18 Oct. 1949	10°33′ N.	126°26′ E.	1	(2)
B-1080	do	10°55′ N.	128°27′ E.	3	(2)
B-1083	19 Oct. 1949	12°44′ N.	130°12′ E.	1	5.2
B-1110	18 Nov. 1949	11°38′ N.	128°38.5′ E.	1	4.8
B-1111	19 Nov. 1949	11°23.5′ N.	123°20.7′ E.	1	(2)
B-1113	do	11°39′ N.	123°02′ E.	2	4.9–5.1

[1] Damaged.
[2] Distorted.

FIGURE 28.—Localities in Philippine waters from which undetermined tuna and tuna-like larvae were collected.

SUMMARY

Within an area of 810,000 square miles the Philippine Fishery Program of the United States Fish and Wildlife Service made 463 larval fish and plankton tows. From these collections, 1,842 specimens of tuna and tuna-like larvae were separated, and the larval forms of 5 genera and 4 species identified: *Grammatorcynus bicarinatus*, *Neothunnus macropterus*, *Katsuwonus pelamis*, *Euthynnus yaito*, and *Auxis* sp. (?). There are 15 genera and 21 species of tuna and tuna-like fishes recorded from Philippine waters, and the larvae of 10 genera and 16 species remain unknown. Until these unknown forms are collected and studied, the specific identification of the larvae of this group will remain a difficult and complex problem.

In spite of the abundance of material collected, many small specimens could not be identified to species. Until a complete series, throughout the size range of each species, is available, accurate determination of the small forms will not be possible. In general, Kishinouye's (1923) taxonomic nomenclature is used in this bulletin, although the tuna and tuna-like fishes may also be classified according to Herre (1950), Berg (1940), or Jordan (1923).

Based upon the seasonal distribution of larvae in the present collections, it appears that the most intensive spawning occurs during December, January, and February, and that June and July represent the period of least spawning. Although it was impossible to conduct periodic reexaminations of any specific area to determine fluctuations in the abundance of tuna-like larvae, six irregularly timed trips to the Sulu Sea helped to confirm the above data. On these trips tuna-like larvae were taken most abundantly during December and January, while June and July were the least productive. Comparison of catch records with surface water temperatures during these trips shows that the greatest number of larvae was taken at periods of the lowest water temperature and the least number was taken when the temperature was high. No attempt has been made in this bulletin to discuss the ecology of the tuna-like larvae, either as a group or as species.

Tows made during the hours of darkness, 1800 to 0600, produced more larvae than those made in daytime, 0600 to 1800. During the day, 87 of the 250 plankton tows made (34.7 percent) were successful, with an average of 1.78 specimens per tow. Of the night tows, 105 of 212 tows made (49.6 percent) captured larvae. The average number of specimens for each night haul was 6.55. A total of 1,395 larvae was collected at night and 447 during the day—or 75.8 percent of the total specimens were taken after dark. Night is not only more productive of specimens, but it seems that larvae are then more widely distributed. It also appears that there is some vertical migration downward during the day and a return to the surface at night.

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