# 16.—ON THE FOOD OF THE MENHADEN.

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The studies of the menhaden (*Brevoortia tyrannus*) upon which this paper is based were made at the station of the U. S. Fish Commission at Woods Holl, Mass., during the summer of 1893, the material for this purpose having been collected in the same general region between July 10 and September 10. Menhaden were comparatively scarce in this vicinity during the period mentioned; no specimens were obtained from the open waters of Vineyard Sound and very few from Buzzards Bay, but in the smaller tributary bays, brackish-water estuaries, and shallow lagoons they were present, and sometimes abundant, as in the mouth of the Acushnet River, at New Bedford, where they spend the entire summer within a comparatively small area. The same may also be said of most of the other brackish-water inlets investigated, as explained below.

The material thus studied is therefore quite sufficient to demonstrate the general character of the food of this fish, together with some of the details. It also illustrates the mechanism by which the food is obtained; and leads finally to some understanding of the organisms of these inshore localities as bearing upon the life-history of the menhaden directly, both as to the time and place of spawning, and as furnishing an appropriate food supply for both adult and young fry—within much protected areas.

The food of the menhaden is to be found in the unicellular organisms, both vegetal and animal, which swarm in all surface waters, together with the smaller crustacea and other free-swimming forms which there congregate, and there are reasons why the regions here considered—the brackish, even almost fresh, waters of broad shallow estuaries and inlets, connecting with the sea only by narrow channels—are very important as affecting the kind and abundance of the various microscopic organisms used by this fish as food. It is here that the fresh-water streams are first brought into the ocean, bringing with them a new source of the inorganic materials—in solutions drained from large land areas—which are so essential to the growth of vegetal cells and animal tissues. By these streams also are brought a wealth of fresh-water microörganisms of the most important nature, especially the *Protophyta*, which thus lend an additional source of food material to the individuals already upon the ground, or find in them new victims for their own sustenance. Salt-water organisms are also brought in with each tide, giving a new intensity to the struggle; it is the common

NOTE.—The paper read by Mr. Peck at the Fisheries Congress was a brief of a report then under preparation by him. The full report, having since been completed, is presented here in lieu of the abstract.

meeting-ground for both salt and fresh water forms, with constant additions from each source, resulting in the closest interaction of all, and the consequent thriving of some particular forms.

Again, the purely physical conditions tend to make these inlets an important swarming-ground for unicellular life, together with the many organisms depending in close connection upon it. The depth of the water is never great, and it is therefore the first to be warmed in the springtime, and is most completely warmed in the summer. The sun's rays penetrate to the bottom and are again reflected; bottom organisms flourish well, contributing a new class of free-swimming larval and adult material. Great banks of eelgrass, lying half exposed at low tide to the summer sun, are hotbeds of growth, and harbor an untold complexity of minute organic forms which often cover each blade of the grass with a living slime. The meshes of our gill nets left down during one night were in many cases coated over with the greenish and brownish algous slime gathered by the flowing of one tide through them. These localities are also (according to all the data available at present) the protected retreats into which this species of fish retires at its spawning season in the early summer, and in which the earliest stages of the young are passed.

These minute organisms furnish directly the food of the menhaden, not only within the limits of these brackish-water inlets and estuaries where the spawn is left to develop, but also wherever the fish is found in the more open coast waters. The whole food supply of this fish is obtained by filtering out from the surface stratum of water the organic life there suspended.

The mechanism by which the menhaden secures this character of food is admirably fitted for such a purpose in the high specialization of the "gill-rakers," which are so complete as to render the whole pharyngeal cavity capable of filtering large quantities of water, which the fish takes in—as has often been observed—by swimming actively in circles through the water, with widely-opened mouth and expanded opercula.

I have given in plates 1 and 2 five figures to illustrate this mechanism. Fig. 1 is an outline (two-thirds natural size) of the adult menhaden in its attitude of swimming through the water for food; in the pharyngeal cavity, underneath the opercula, are indicated the positions of the five gill-arches (*1*, *2*, *3*, *4*, *5*) of the right-hand side of the animal; the five corresponding gill-arches of the opposite side of the throat cavity are omitted in the diagram. In fig. 2 are represented the five gill-arches, with all their parts, of a somewhat larger specimen (drawn two-thirds natural size) removed from the fish and placed in order, one behind the other, in a series, of which *A* is the most anterior, the others, *B*, *C*, *D*, following to *E*, the small rudimentary one, which is the most posterior. Attached to the axial gill-arches *1* to *5*, upon the anterior edge of each, is the row of fine stiff gill-rakers *a*, *b*, *c*, *d*, *e*, arranged in a close parallelism like the barbs upon the shaft of the bird's feather, which, indeed, they closely resemble in appearance. These are relatively very long, reaching far forward upon the inner face of the mouth cavity on the right-hand side, the left side of course having a corresponding set attached in like manner to the bony gill-arches as axes. Projecting backwards from these gill-arches are also the regular double-rowed lamellæ of branchial filaments *m*, *n*, *o*, *p*, the respiratory apparatus proper of the fish; the last gill-arch *5*, however, carries no branchial filaments.

If now these be telescoped together into their natural position in the sides of the mouth cavity of the fish, then *A* will be the most anterior; *B*, *C*, *D*, *E* will follow in a closely arranged series; the branchial filaments *m*, *n*, *o*, *p*, each overlapping its next posterior neighbor, will be next the operculum which covers them. In like manner the gill-rakers *a*, *b*, *c*, *d*, each underlapping its next anterior neighbor, will cover the the interior surface of the mouth cavity, and this in a very perfect manner. The gill-rakers of *A* all project straight forward (*a*); those of *B* (*b*) upon the upper section of the gill-arch curve upward, as in fact the remaining members of the series all do (*b*, *c*, *d*,) in order to reach up to the upper section of each preceding gill-arch.

Reference to the diagram (fig. 1) of the gill-arches in place will show that they project downwards into the roof of the mouth, each one hanging lower down than the one preceding it; and the curving upward of the gill-rakers upon the upper section of each of the three arches (*2*, *3*, *4*) makes such an arrangement as to completely cover the roof of the mouth with these curving gill-rakers from the protruding gill-arches. Upon the upper section of gill-arch *3* is indeed a double row of gill-rakers; the regular series of upward curving ones—the continuation of *c* projecting from the upper segment of this arch—to which is added another one (*x*) projecting downward and backward to meet *y* of the next posterior series. (Part of the series *c* is omitted in the drawing in order to expose series *x* to view.) The lower edge of *x* therefore fits into the edge of series *y*, which curves abruptly upward to meet it. The rudimentary gill-arch *5* carries a short and stiff row of gill-rakers only. If the mouth of a menhaden be opened the observer is confronted by a throat cavity completely lined with a layer of these beautifully adjusted lamellæ of gill-rakers, overlapping each other in the most perfect manner—as I have attempted to explain in the foregoing; their function, namely, that of extracting food from the water, is as perfectly performed as the sequel will, it is hoped, aid in showing.

The water passing into the mouth of the fish will pass through this system of gill-rakers and make its exit posteriorly from under the opercula. The water passing through the gill-slit between *m* and *n* will be filtered by the series of gill-rakers *b;* the water passing through the gill-slit between *n* and *o* will be filtered by *c;* the water passing through the gill-slit between *o* and *p* will be filtered by *d*, *y*, *x;* in each case, of course, the upper portion of the gill-arches with their filaments will be bathed by a large part of the water as it passes through. That the column of water in so passing through this apparatus may be deprived of the organisms living in it is made evident by the finer structure of the gill-rakers themselves, as illustrated in the other figures of plate 2. They constitute rows of thin elastic bony blades arranged upon the anterior edge of each gill-arch, as before described; fig. 3 represents the basal part of six of the gill-rakers attached to their support; their full length is not, however, given. Each individual blade—covered with a delicate epithelium, in which are mucus and large-branched pigment cells—is provided with two rows of hooked barbs, one row upon either of its sides, which so project in between from all of the adjoining gill-rakers as to guard each interspace with two rows of these barbs. A diagram of these gill-rakers in cross-section is given in fig. 5, showing the attachment of the barbs to the exterior (toward the operculum) edge of each gill-raker blade, allowing them to project inwards toward the current of water passing through the mouth cavity of the fish. Finally, in much higher magnification, 178 diameters, are given, fig. 4, six of the hooks or barbs as they are attached to a gill-raker blade, showing that each of these, again, has a serrated tip. Fig. 4 is drawn to the same scale as the organisms figured in the other plates hereafter described, whence it is evident that the organic materials are easily secured by such an apparatus—the fineness, elasticity, strength, and least possible resistance of which are evident.

The whole interior of the mouth is always abundantly supplied with a mucous secretion, which aids in the accumulation of the fine food particles as they are strained from the water, and also aids no doubt in conveying them back to the œsophagus. There is also a delicate fold of the mucous membrane running along each gill-arch at the base of the series of gill-rakers, making there a deep channel, but whether there are definite ciliated tracts with this function of conveying solid particles is not as yet known. One always sees, moreover, in examination of these barbs, more or less food material clogged in their meshes, showing again the manner in which it is lodged by them. The cavity of the back part of the pharynx of the fish narrows abruptly to an apex which, guarded by a constrictor muscle, opens directly into the folded stomach of the fish.

The comparatively empty condition of the menhaden stomach has often been noted, as also the presence of a greater or less quantity of what appears to be a dark greenish or brownish mud, with a variable quantity of copepods and small crustacea intermixed, although these latter may be almost entirely absent. This apparent mud, however, is made up of the various organic matters which are always suspended in surface waters, and which the fish, by means of the filtering mechanism of gill-rakers just described, has removed from the water in which he has been feeding. This may be demonstrated not only by observing the habits of the fish when living, and by a study of the gill-rakers, but also by collecting through a filter the organic matter suspended in a given quantity of surface waters* from the localities where the fish are taken, and then by comparing such a filtrate with the stomach contents of the animal. Studies carried on in this comparative manner show very well how wide a range of microörganic forms contribute to the sustenance of the menhaden, how they are to some extent localized, and finally some of the ways in which they interact upon each other, besides serving as food to the fish.

One of the richest feeding-grounds of the menhaden studied during the season was in the estuary of the Acushnet River at New Bedford, Mass., as it was here also that the food in the earlier part of the season was of the most complex character. In a mass of food taken July 12 from the stomachs of two dozen fish one could readily find a few small annelids of the genus *Nereis*, measuring about a half inch in length usually; a few rotifers of the genus *Notomata* as nearly as they could be identified; quite a wide range of the smaller crustacea—small amphipods (*Gammarus*), young schizopod shrimps, a few ostracoda (*Evadne*), a few *Zoea* larvæ, with quite abundant *Nauplius* larvæ of different species. It may here be stated of the above-named organisms, that they are more abundant in fish taken during the night. I have never

* This was done in the course of this investigation by means of a filter, such as is used by Mr. G. W. Rafter, of Rochester, the Board of Health of Massachusetts, and the Laboratory of the Western Division of the Boston Waterworks, etc., made from a large funnel whose tube is closed at the lower end by a coil of fine wire gauze; upon this plug of gauze rests a ½-inch stratum of fine white sand upon which the organisms collect as the water filters through; from the sand the material is washed out in a given small quantity of water.

noticed young annelids in fish taken in the seine by daytime, while the crustacea are also less abundant; especially noticeable is the lack of schizopod shrimps, the fewer copepods. But by far the most constant features of the menhaden food in this district are the unicellular elements in it, especially the unicellular plants, and of these the various genera of the family *Peridinium* easily predominate.

In plate 3, fig. 7, is represented a camera drawing of one field of the microscope, under a magnification of 178 diameters, of the organisms as they appear in the material collected from the surface waters of this estuary by means of the sand filter just described. The great majority of the organisms are *Glenodinium*, some of the most characteristic of which are shown at *p*, fig. 7, in the various positions of the cells. A good description of the characteristics of the marine *Peridinium* and the life-history has been given by George Klebs,* and it is easy to make out the general plan of their structure in this material. There are also taken at the surface here other pear-shaped alga swarm-spores *r*, besides many diatoms, of which, however, only a few are here shown. The *Infusoria* are an important factor in this surface material; some are the small green (*t*) which are very numerous; most abundant, however, are the small bean-shaped flagellates (*s*), which go winding their way in among the other material upon the slide when all else is motionless. All these organisms finally are mixed together in a greater or less quantity of amorphous matter—flocculent bunches of greenish and yellowish color, just such as are to be found in filtering any surface waters. Dr. W. T. Sedgwick tells me that in his opinion the color of this is due to the presence of bacteria masses of the *Zoöglea* form. There is also no doubt the detritus from disintegrating organic material of many kinds. All this matter is highly phosphorescent when concentrated upon the sand in the tube of the funnel in the course of filtration, as may be seen by disturbing it in the darkness.

Compare now with fig. 7, fig. 8, which represents in a similar manner one field of the microscope drawn with camera, exhibiting the same organisms taken from the stomach of a menhaden; the fish was feeding in the locality just mentioned where the surface waters were filtered. The same *Peridinium* is present and in the same large proportion to the other forms of living material, except that the smallest organisms—infusoria, etc., of fig. 7—do not appear in this material to any great extent. This may be due to the fact that the very smallest actively moving organisms may pass through the meshes of the pharyngeal filter, which may be readily conceived on account of their minute size, or they may be so mixed up in the mucous and amorphous matter in the fish's stomach as to escape detection to a great extent. It is easy to see the complete identity between living organisms filtered from water by mechanical contrivance and those secured by the menhaden feeding in the same waters by means of his anatomical specialization, giving a demonstration that the menhaden is a surface feeder—taking the organisms suspended in the water in a very complete manner.

It must not be imagined from the foregoing figures that the waters there contain no other organisms than *Peridinium;* the percentage of diatoms is very great, not to mention the annelids, rotifers, and crustacea, before enumerated, which latter were (except the crustacea) found only in this locality in the stomach contents of the fish. In fig. 16, pl. 7, are represented some of the more important diatoms selected from the food taken from several fish in this locality; there is also an occasional alga thread,

*In the Botanische Zeitung, Nos. 12 and 14, 1884.

as also oscillatoria threads. One large foraminifer was also found in the food, belonging to the genus *Discorbina*.

Applying the same methods of procedure—*i. e.*, comparing the organic matter filtered from the water with that found in the alimentary tract of the fish—to other localities, it will be seen that the organisms have certain local variations, with which the stomach contents of the menhaden are again in close agreement. For instance, the fish taken within the southeastern corner of Buzzards Bay have contained within their stomachs organic food-stuffs which agree completely within themselves and with the microörganisms free-living in the water where they were taken. It may be observed that the quantity of food here present was much less than in those fish which had been feeding in the brackish waters of other regions; indeed, one fish which had taken its food during the night at New Bedford—which therefore included a large proportion of the smaller crustacea—contained four times as much food as ten fish taken in the pounds in this corner of the bay. This is an extreme case, however, for a fish feeding at daytime in the estuary contains less food than one feeding at night; while the Buzzards Bay fish, entrapped in a pound, may have digested up a large part of his stomach contents during the night before being taken for examination. But it is undoubtedly true that the food supply of a fish in the open waters of the bay is less than that of one feeding in the estuary before named. This is evident by comparing the organic material filtered from a given quantity of surface water from each region; also from the contents of the stomach, and from the relative weight of fish of the same length in the two regions—the fish from the bay weighing less for their length than the fish from the Acushnet estuary or any other brackish-water locality. An illustration of the extent of these differences is given in the outline drawings, one-half natural size, of plate 8; fig. 17 was from a fish taken July 20, at Woods Holl, Mass., in Buzzards Bay; fig. 18, from a fish taken August 25, at Waquoit Bay, a large protected inlet with narrow opening to the sea, in which the microörganic life was very abundant. The organisms from the water of Buzzards Bay may be judged from plates 4 and 5. The stomach contains little food and a great deal of mucus, just such as is secreted in the mouth of the fish, but the microörganisms are very characteristic. Those of three different positions of the microscope are gathered into fig. 9, giving a characteristic idea of the material in a given fish's food. There are new forms of the *Peridinium* type, the large sculptured *Peridinium* sp., at the upper edge of the field *p*, as well as the large, smooth, pinkish *Peridinium* sp. at *p* in the left central part of the field; also at *r*, half of the very much elongated *Ceratium fusus*.

Perhaps the most characteristic element of this locality, however, is the large infusorian *t* of the genus *Codonella*, of which several species are found. A review of the structure and systematic arrangement of these important organisms may be found as given by the studies of Geza Entz upon this group.* Also by the studies of Dr. Eugene V. Daday.† The *Codonella* here found were of the species which are invested with a test in which calcareous nodules are imbedded, and were exceedingly abundant in the food of the menhaden taken in this region. There is also the diatom (*e*) with the flatiron-shape, and the infusorian *m*, which hereafter becomes one of the most constant features of the menhaden food. In the same manner fig. 10 shows other representative organisms of this region, taken from fish entrapped at Woods Holl, on the

* Mittheilungen aus der Zoologischen Station Zu Neapel, Bd. 5, 1884, p. 389. Ibid. Bd. 6, p. 200.

† Mittheilungen aus der Zoologischen Station Zu Neapel, Bd. 7, 1886–1887, p. 473.

bay side. At *p* is the same *Peridinium*, at *h* the infusorian *Dinophysis*, the same abundance of *m*, a *Codonella t*, some of the diatoms at *d*, all gathered into this figure from two fields of the microscope.

Organisms from the stomach of a fish taken off Naushon Island, at the Weepecket Islands, are indicated in fig. 11—from a single field under the microscope. The *Tintinnodea* (*t*) were remarkably abundant, the same diatoms as before were also very numerous, as also the *Ceratium fusus*. That these of the three preceding figures are the common unicellular organisms of the surface waters of this region of the bay in which the fish were taken is shown in fig. 12, which represents some of the surface organisms filtered out of the water of the bay by means of the sand filter before described. There are the same *Peridinium p*, *Tintinnodea t* and *v*, the same infusoria *m* and *h*, the same diatoms *Nitzschia*, *Synedra*, *Concinodiscus*, *Navicula*, etc., *d*, together with others not figured in the food material as found in the fish's stomachs, noticeably the beautiful *Chætoceros*. It is worthy of mention that the *Tintinnodea* figured were relatively more abundant in the stomachs of the fish than in the filtrate from the surface waters, and is perhaps to be explained by a different depth in which the fish were feeding; or the fish having in every case fed at night, while the water filtered was taken at daytime, these infusoria may have removed from the immediate surface at the time the sample was taken. In the food here figured the crustacean elements of it have been neglected, both because it is sometimes quite scanty and at other times very abundant, even in the same locality, and is of the same general character in all the localities studied, preëminently copepods, larval and adult. The minute crustacea are of course a favorite food of the menhaden, but no attempt has been made to illustrate it with the other organisms with which it is associated in the stomach of the fish. That is to say, those portions of the field were selected for figuring in which the crustacea were absent.

I shall, finally, illustrate this same point of the localization of littoral surface organisms by figures offering a similar comparison of some of the unicellular surface organisms from a very long lagoon of brackish water at the eastern end of Marthas Vineyard (at Vineyard Haven), in which menhaden in four different lengths, or stages of growth, were taken, showing again the identity of those organisms in the alimentary tract of the fish with those in the surrounding surface waters in which they were feeding. There is considerable difference in the prevailing types, although, of course, many of the species are common to it and all the other localities studied. Some of the organisms filtered from the surface waters are represented in fig. 13, selected from various parts of a single slide of the microscope. The diatoms are beautifully represented by the chain *d*, composed of very large individuals unknown to me; these are very abundant in this locality. Another chain, *g*, of a species unknown to me, is also quite common, as is also the genus *Lauderia* (*f*). The *Peridinium* family is represented chiefly by the large, smooth, pinkish form *divergens*, with an occasional *Glenodinium*, *r*, such as was found at the Acushnet River locality. At just below *a* is represented the empty cell wall of a small vegetal organism, unknown to me, having a peculiar rounded right-angled triangle shape, with very thick walls. The *Tintinnodea* are extremely abundant, too, in this locality, presenting a great variety of species; at *w* is a *Tintinnus*; at *v* a peculiar kind, with a spiral marking and 2 whorls of an expansion or flange on the test; those forms represented at *t* and *c* are also common. Taken altogether, this lagoon exhibited one of the richest surface faunæ studied during the summer and like the others seemed to grow even richer as the early autumn approached.

Some of the organisms in the stomach of a young fish—60 millimeters in length—are shown in fig. 14; the same genera of diatoms are present, the same *Peridinium* and infusoria, the same organism, *a*, as were found in the preceding instance, from the water filtered artificially. In an adult fish of this locality are also found the same organisms as are here portrayed in figs. 13 and 14; especially in some fish are great numbers of the *Tintinnus*. If now reference be made to fig. 6 (plate 2), an idea may be given of some of the most important organisms found in this same lagoon at Marthas Vineyard, but in a large pond shut off at its extreme upper end from the main body of water except for two very narrow sluiceway connections. Fish were here taken measuring 100 millimeters in length, and their food products represented in part in fig. 6. The lower half of the field is an exact drawing of the number (in a single field of the microscope) and position of the very abundant vegetal organism heretofore mentioned; it comprised far the greatest part of the food material. In the upper half of the drawing are represented some of the other organisms which were of common occurrence in the same material. All of these are alike found in the surface waters, and in the menhaden stomachs of this interesting locality. In these surface waters were also found many threads of fungous mycelia, also oscillatoria threads in considerable quantities.

It thus appears that young menhaden, as soon as they can be secured, indeed, in the earlier part of the season, consume the same kinds of food as the adult fish, and this holds true of the other localities considered in this work. They consume the copepods also, like their parents, in such numbers as these crustacea appear. Indeed the stomachs of the young fish show these organic food constituents in the clearest manner, since there is less mucous and amorphous matter mixed up with them. The young fish from the Acushnet estuary contain *Glenodinium* in the same abundance as do the adults, while the young fish of each locality examined led to the same conclusions; and figures drawn from the material upon the microscopic slide would not differ essentially from the figures just described.

The food of the menhaden is not confined to the brackish-water inlets, however, for by filtering the clear blue surface waters in the open channel of Vineyard Sound one can at this same season gather a very interesting array of the microörganisms such as have been here considered. In fig. 15 are represented a few of the common forms there secured, which in some respects are different in their relative kind and abundance from any other locality examined. The diatoms are represented by the large *d;* indeed, these were very abundant in the filtrate, insomuch that a brownish yellow color was given to the whole mass by reason of them. There is also very commonly the large *Chætoceros g*. The infusorian *h* (*Dinophysis*) is very common; the infusorian *m* is also common. The *Peridinium* group is represented by the very large *Ceratium tripos*. A great deal of *Ulothrix* (?) *n* is also common in this water. The copepod *Nauplius*, *y*, is given simply to indicate its relative size to the unicellular material.

The drawings can of course give no conception of the delicate sculpturing, coloring, and beautiful contour lines of these organisms, but it is hoped that the relative size may be gathered from them, as also some graphic idea of the general make-up of this interesting food and something of the form of its varied constituents. Nor has a detailed account of the systematic identification of all the organisms been attempted, but it is hoped that enough has been given to indicate to those who may be interested some of the more important elements of the protozoan and protophytan life in brackish and inshore waters. The main object of this paper is to show the importance of those groups to the life-history of the fish in question. Three other localities of similar characters (in the same coast belt of this region) were periodically studied during the greater part of the summer, in which the same general character of surface material was found and in which menhaden were feeding. In all cases, also, the same results were obtained as have been heretofore descrided, *i. e.*, the material from the alimentary tract of the fish was entirely comparable to that of the organic filtrate from the surface water. Such then is the general character of the food of these fish, and some of its differences according to littoral localities. It varies in amount also, as has been shown, but any of the coast waters contain an abundance of this microörganic life for their sustenance, as may be determined by testing a few liters of the water.

If now the mouth of an average menhaden be opened as in its natural position when feeding, its outline will form an ellipse, of which the area will be about 1.1 inches; and if his rate of progress through the water when feeding be 2 feet per second (as I have estimated from watching the habits of a small school confined in a large pool), then the fish feeding continuously would be able to strain a column of water 1,440 inches in length of the size of the fish's mouth—*i. e.*, 1.1 inches—each minute, which column of water at the surface of the Acushnet River would in July contain 6.8 gallons of water and about 3.4 cubic centimeters of the organic filtrate, such as is found in the stomach of the average fish. The average amount of food material in the stomach of the fish feeding at that time is about 3 cubic centimeters, which, according to this estimate, would be obtained from less than 7 gallons of water, and which the fish could, therefore, extract in about one minute. Of course these quantities are only estimates; the menhaden does not feed continuously, and it may be that all the water does not pass through the gill-rakers at the rate the fish swims, so that the amount of water actually filtered is doubtless considerably less; many of the smaller organisms also may escape through the meshes of the gill-rakers, so that it may take the animal longer to extract the given amount of material from the surrounding medium, while my estimate of the average amount of food in a normal fish stomach is very low for this particular locality. On the other hand, the animal swimming with widely-open mouth against the water brings some pressure to bear, and so aids in the rapidity with which the water passes backward through the pharynx—so that the above low-estimated amount filtered in a given time is by no means unreasonable for such a time as the fish does really feed.

But the estimates of the quantity of organic matter actually present in the water are certainly reliable; and allowing for all shortcomings on the estimated capacity and movements of the fish, there is still a wide margin in favor of its ability to gather a great amount of food in a short time.

The passage of the food through the alimentary tract is, however, probably very rapid, and a large quantity of this kind of food must be needed by the fish; in favorable localities the whole intestinal canal is gorged with this material. The quantity of such food, moreover, is illimitable, each cubic foot of water is charged with it, and rapidity of increase of the unicellular organisms in a geometrical ratio—their life-history being measured almost by moments—is such as to insure a stable basis of existence to those species depending upon them. Indeed, it is little wonder that these fish are so fat when their food supply is considered.

Another important consideration in the make-up of the menhaden food is its vegetal character to so great a degree. The predominance of the many species of diatoms and *Peridinium;* the swarm spores, oscillatoria, and fungous threads contribute directly to the food of the animal itself, and indirectly through the large infusoria and copepods. Of the large family of infusoria—*Tintinnodea*—so abundant in the foregoing descriptions of the menhaden food, Daday says: *

> Im Haushalte der Natur spielen sie durch ihre Gefrässigkeit eine ziemlich bedeutende Rolle, indem sie ausser den kleinen Diatomeen, Algen und anderen Pflanzenresten auch viele verfaulte organische Stoffe verschlingen.

He also goes on to say that they do not shun microscopic animals, but repeatedly can be found having eaten *Dinoflagellates, Peridinium* and *Dinophysis;* even their own relatives—*Codonella, Tintinnopsis,* etc. This is also no doubt true of many of the other infusoria gathered by the menhaden. In the figures of the infusoria of the Gulf of Naples† Entz represents very many of these organisms with diatoms within their cytopasm. The copepods, which are the most important animal constituent of the food material, feed, I am very sure very largely upon the same vegetal diet in these localities here considered as is taken by the menhaden. The alimentary tract of the copepods is filled with a greenish-yellow colored mass of material, in which one may often identify the small vegetal cell so abundant in fig. 6 (plate 2), which by reason of its minuteness has escaped the crushing up in the process of feeding by the animal. In an arm of Childs River, Waquoit Bay, it is almost certain that the abundant copepods of the surface water were filled with the small *Raphidium polymorphum,* which, together with very many other forms of oscillatoria, made a large part of the material gathered by the fish, which organism was so abundant in the stomach of the menhaden. Another important place in the elaboration of this vegetal microörganic food supply is undoubtedly filled by the bacteria, whose abundance and even presence are so unsuspected in the ordinary study of microörganisms of surface waters. Dr. H. L. Russell, speaking of the diminution of land bacteria as one leaves the shore and proceeds into dense sea water, says: ‡

> Die gewöhnlichen Spaltpilze, welche im süssen Wasser und im Erdboden vorhanden sind, werden durch die Thätigkeit des Seewassers und der darin enthaltenen Mikroorganismen zerstört.

Dr. W. T. Sedjwick tells me that in his opinion the bacteria are freely used as food by the larger infusoria. The many bacteria in the so-called amorphous matter and those brought by fresh-water streams into brackish water do doubtless contribute no small element to the food supply of the infusorial organisms there swarming. Vegetal diet upon the unicellular plants is, therefore, very plainly to a great extent at the basis of the menhaden food; § while the fish subsist very largely upon those organisms directly, gathered by their pharyngeal filters, and indirectly upon the same

* Monographie der Familie der Tintinnodeen, p. 512.

† Ueber Infusorien des Golfes von Neapel, pl. 20-22. Mitt. aus der Zool. Station zu Neapel, Bd. 5.

‡ Untersuchungen über im Golf v. Neapel lebende Bacterian. Zeitschrift für Hygiene und Infectionskrankheiten, Bd. 11, 1891, pp. 167, 213.

§ See also Ryder, U. S. F. C. Bull. 1878, p. 242. The Protozoa and Protophytes considered as the primary or indirect source of the food of fishes.

material as it comes to them through the copepods, the various free-swimming larvæ, and infusoria.

Such being, then, the primitive character of the food supply of the menhaden, its economic relations are very important; it arrives first hand at a food supply which is the most stable, the most abundant and widely distributed of all foods, and yet so unavailable to the great majority of other species. The wide distribution and vast extent of the schools of this fish (which have been so remarkable in former years), testify to this fact, for no matter how many are aggregated together in a given area the food supply is adequate. At the same time the menhaden comes into no competition with the other food-fishes. In all the food products in the alimentary tracts of specimens examined during the time named, not a trace of vertebrate tissue was found; their presence does not threaten directly the life of any other vertebrate, nor indirectly do they bring want to others by appropriating too much of their food supply. In one instance this summer—at Hadley Harbor, Naushon Island—a small school of menhaden was seen rising to the surface directly under a school of young "silversides." The suddenness of the maneuver on the part of the former fish sent the minnows leaping out of the water and scattering in all directions, just as when the school is so invaded by enemies; as the silversides collected again, after a few moments, at the surface, at a little distance from the former spot, the action was repeated by the school of menhaden. A number of these latter were then captured and examined, but in no case, of course, had the minnows themselves been taken as food, while the large proportion of copepods in the stomachs of the menhaden would indicate that they had found their prey located by the movements of these small surface-feeding minnows. Their stomachs also contained, besides the usual quantity of microörganic life, diatoms, infusoria, and the like, which are abundant in the brackish waters of that beautiful and quiet retreat.

Not only, therefore, do the menhaden not compete with other fishes for food, but they themselves form an important factor in the food of other fishes, as has been so often observed in the bluefish, bonito, and squeteague; making available through their own life-history favorable conditions upon which the other economic fishes are borne and satisfied; bringing to them directly an elaboration of this primitive food supply here considered. To just what extent the menhaden are eaten by other food-fishes has not yet been entered into in this investigation, but evidences of its importance as bait are everywhere at hand, and for this reason, if no other, its place is an exceedingly important one in all questions involved in the study of hook-and-line fishing. The eagerness of the fishermen after menhaden for bait has been a most constant feature of the expeditions made by us during the summer after the material used in this study. One sees in the common opinion something more than a general preference for such bait; it is a real necessity in their equipment for work.

The relations of every individual organized being are so complex, the interaction of its species upon others so intimate, that the life-history of every being must have a very large circle of effects—visible and remote—not all of which may act in a directly beneficial way for all of our immediate specialized wants. So it may be with the menhaden, as with any other fish. In its method of gathering its food it does not, it is true, come into competition with other fish, but the floating eggs and minute embryos of all classes would be of a necessity swept in greater or less numbers into its mouth in those surface waters which were supporting schools of menhaden. Large schools of the latter fish moving along the coast at the spawning season of the scup and sea bass might draw largely upon the floating eggs of the latter and lobster embryos. Large schools of menhaden feeding in the brackish water over rich oyster beds might at the spawning season of the latter diminish materially the chances of so thick setting as might have been otherwise made had the fish not been present to strain so effectively the surface waters, with the chance of securing so many of the floating eggs and very young embryos. A detailed study of just these conditions has not yet been made, but such evidence as we have is negative. Along this part of the coast the scup, sea bass, and menhaden appear to be spawning at about the same time, the last fish having, however, removed up into brackish water retreats away from the other food-fishes. There are, however, large numbers of immature menhaden present which are not concerned with the business of spawning, and of whose movements as they first migrate into these waters very little is definitely known. At the season and localities covered by this work, however, there was no material found in the food products of the menhaden which was derived at the expense of other food-fishes. Nothing, indeed, was found but such minute organisms as are present in all these localities studied, and so abundant and evenly distributed through the surface waters that their quantities could never be materially diminished through being preyed upon by the menhaden. These organisms also are entirely unavailable to the great majority of fishes, but being thus taken directly by the menhaden they serve indirectly in the food supply of the many predaceous species to which *Brevoortia tyrannus* itself becomes a prey. Problems, therefore, which involve the consideration of this last species, with any regulations which are to be proposed for it, are very significant.

It may be urged, finally, that these many brackish-water inlets and estuaries, which so plentifully indent our coast, are regions of especial importance, entitled to the most careful consideration, because they are intrusted with so much embryonic and larval life of the migratory inhabitants of the coast, have such a rich and varied food supply, and are so much protected from the larger invaders. This is the only series of conditions to be treated in oyster-culture, and will prove, no doubt, to be a very important step in the study of many others. Such places, moreover, are the nearest at hand to which all regulations can be the most effectively tried, which can be made the most evident examples for public opinion.

U. S. FISH COMMISSION,

*Woods Holl, Mass., September 11, 1893.*

## EXPLANATION OF PLATES.

PLATE 1, two-thirds natural size:

Fig. 1—Outline of adult menhaden as feeding. *1–5*, gill-arches of right-hand side in natural position.

Fig. 2—Gill-arches with branchiæ and gill-rakers attached, removed from fish and arranged in order; *1–5*, bony arches; *a, b, c, x, d, y*, and *e* are gill-rakers; *m, n, o, p*, branchiæ.

PLATE 2:

Fig. 3—Six of a series of gill-rakers attached to the gill-arch, showing the projecting rows of hooks, enlarged 50 times.

Fig. 4—Six of the hooks attached to the gill-raker, enlarged 178 times.

Fig. 5—Diagram of gill-rakers in cross-section, showing angle at which hooks project from their point of attachment in toward the throat cavity, and the current of water passing out from it.

Fig. 6—Organisms from stomach of young menhaden taken from a pond closed off from lagoon at Marthas Vineyard: *p, Peridinium; d, Diatoms; t, Tintinnodea;* lower half of field drawn with camera from single field of the slide, magnified 178 times.

PLATE 3:

Fig. 7—Organisms filtered from surface waters of the Acushnet river, showing at *p* the *Glenodinium* which is so abundant at this locality; *s*, very small bean-shaped flagellates; vegetal cells are also scattered over the field.

Fig. 8—Organisms from the stomach of a menhaden in these same waters, showing the predominance of the same *Glenodinium; h, Dinophysis;* drawn from a single field of the microscope, enlarged 178 times.

PLATE 4:

Fig. 9—Organisms from stomach of fish taken in Quisset Harbor, southeastern portion of Buzzards Bay; *p, Peridinium*, the lower two large, smooth, pink-colored individuals, having the form of the species *divergens; d, e*, diatoms; *t, Tintinnodea* of the genus *Codonella; r, Ceratium fusus.* Enlarged 178 diameters.

Fig. 10—Organisms from fish's stomach taken at Woods Holl, in the mouth of Buzzards Bay; *d*, diatoms; *p*, a large *Peridinium; h, Dinophysis; m*, an infusorian unknown to me; *t, Codonella.* Enlarged 178 diameters.

PLATE 5:

Fig. 11—Organisms from food in fish's stomach taken off Naushon Island, mouth of Buzzards Bay, at the Weepecket Islands (drawn with camera from single field of microscope); *t, Codonella; d*, diatoms; *r, Ceratium fusus; m*, infusorian(?). Enlarged 178 diameters.

Fig. 12—Organisms filtered from the surface waters of Buzzards Bay, in these same localities; *p, Peridinium divergens; t* and *v, Codonella; d*, diatoms, of which there is a representative of the genus *Chætoceros*, with its long protoplasmic processes; *e*, also diatoms; *h, Dinophysis.* Enlarged 178 diameters.

PLATE 6:

Fig. 13—Organisms filtered from the surface of Lagoon Pond, Marthas Vineyard; *d, g*, and *f* (*f* is *Lauderia*), diatoms in chains; *p, Peridinium divergens; r, Glenodinium; c, Codonella; w, Tintinnus; t*, allied to *Codonella; v*, one of the Tintinnodea unknown to me; *a*, very small vegetal cells. Enlarged 178 diameters.

Fig. 14—Organisms from the stomach of a young fish of the same locality (fish 60 mm. in length). *p, Peridinium divergens; d*, diatoms; *f, Lauderia; h, Dinophysis; m*, infusorian unknown to me. Enlarged 178 diameters.

PLATE 7:

Fig. 15—Organisms filtered from surface waters of Vineyard Sound upon a bright clear morning, August 15; *d*, large diatoms, which were very abundant in the sample of water; *g, Chætoceros; n, Ulothrix zonata* (?); *h, Dinophysis; c, Ceratium tripos.* Enlarged 178 diameters.

Fig. 16—Some of the organisms found in the stomachs of menhaden in the Acushnet River, in the same material figured in plate 3. *g* and *y*, alga threads; diatoms, *a, Triceratium; b, Bildulphia; c, Stephanodiscus* (?); *e, Navicula; j, k, Pinnularia; i*, unknown diatoms; *f, Merismopedia* (alga); *x, Discorbina.* Enlarged 178 diameters.

PLATE 8:

Fig. 17—Outline of an adult menhaden living in Buzzards Bay, taken July 20. One-half natural size.

Fig. 18—Outline of an adult menhaden living in the extreme upper part of Waquoit Bay, taken August 25. One-half natural size. This region was very rich in *Protophyta*, especially *Cyanophyceæ*, also *Copepoda.*

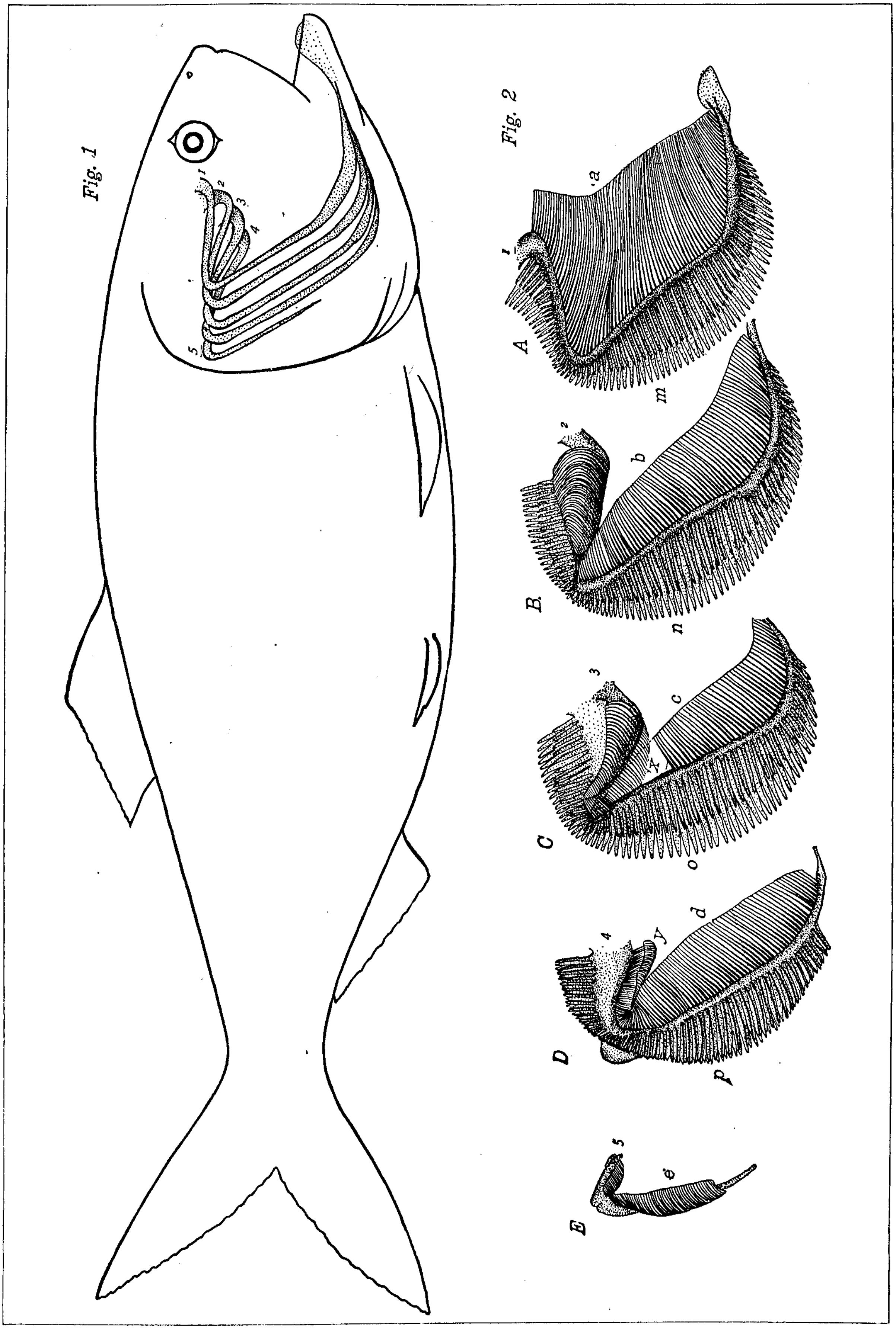


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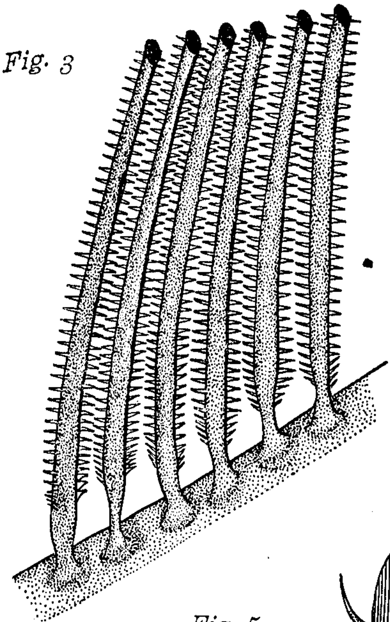
Fig. 3



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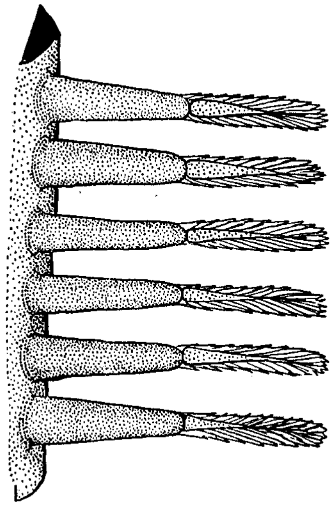

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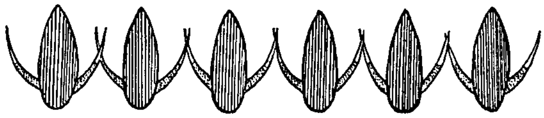

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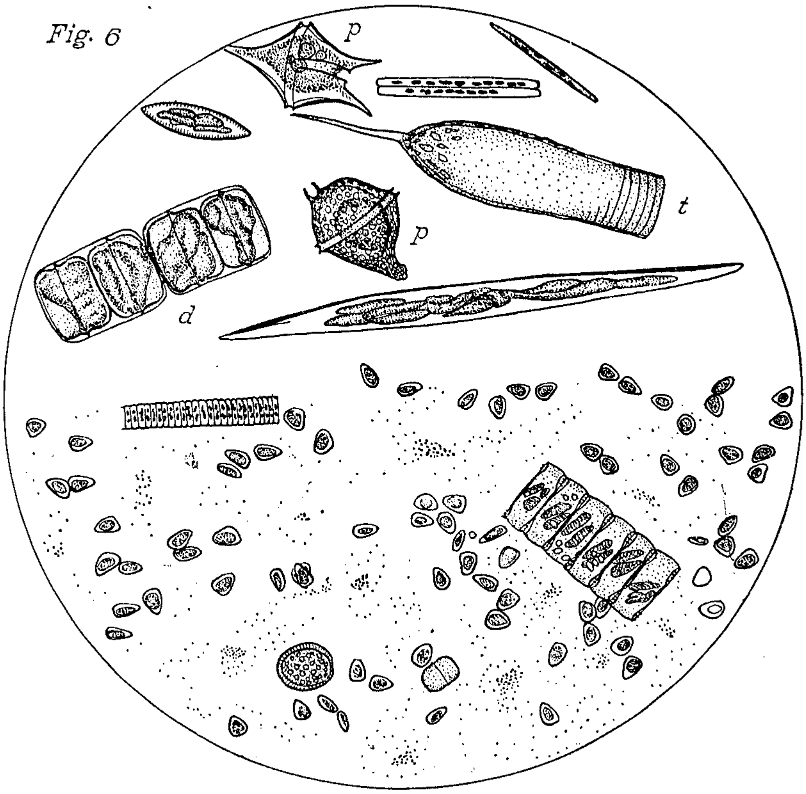


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PLATE 3.

*Fig. 7*

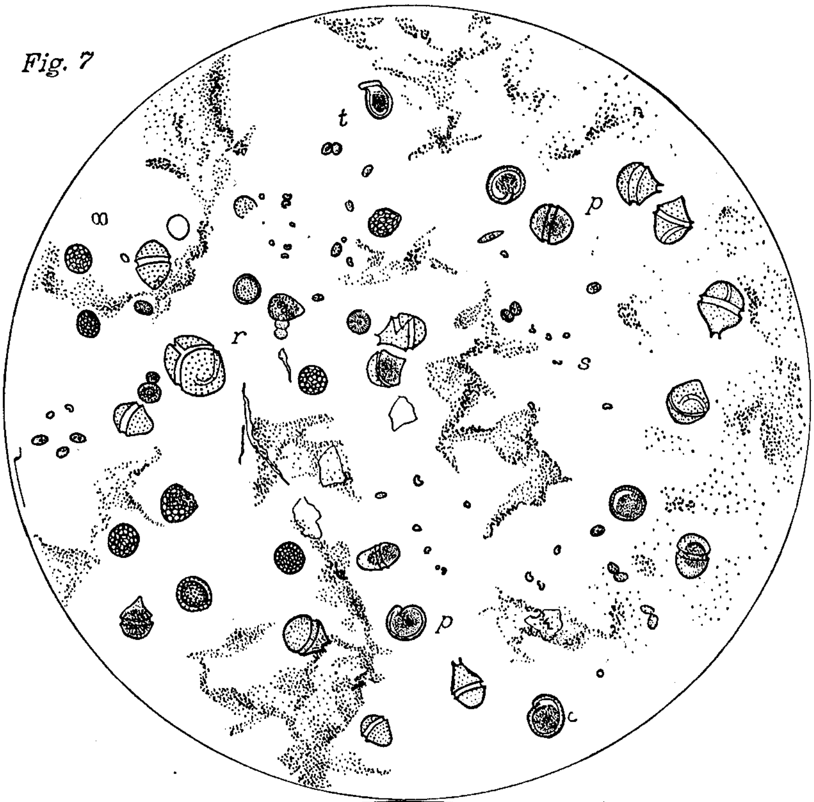


*Fig. 8*

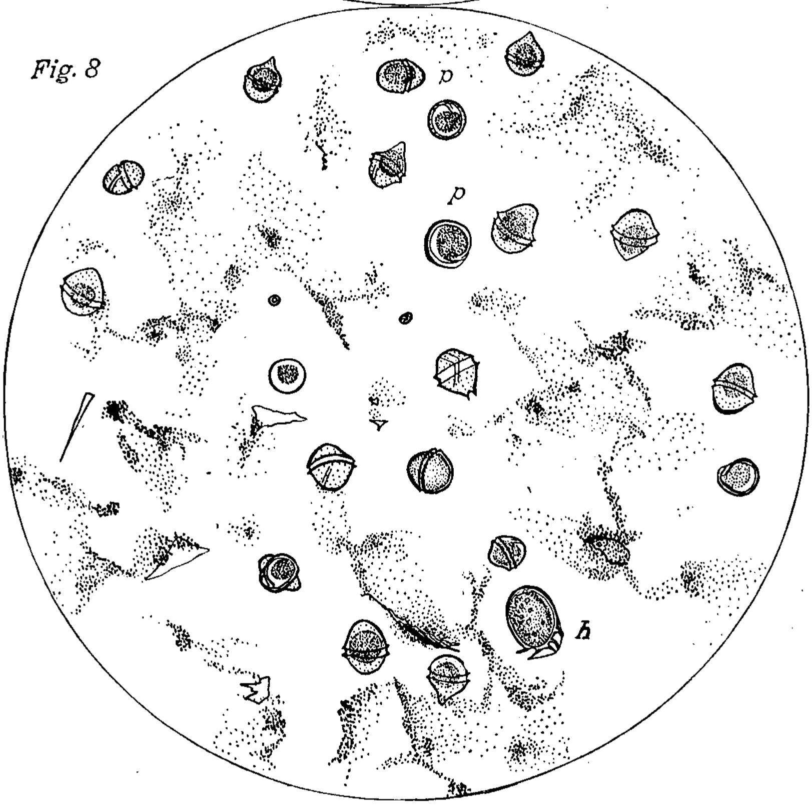


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*Fig. 9*

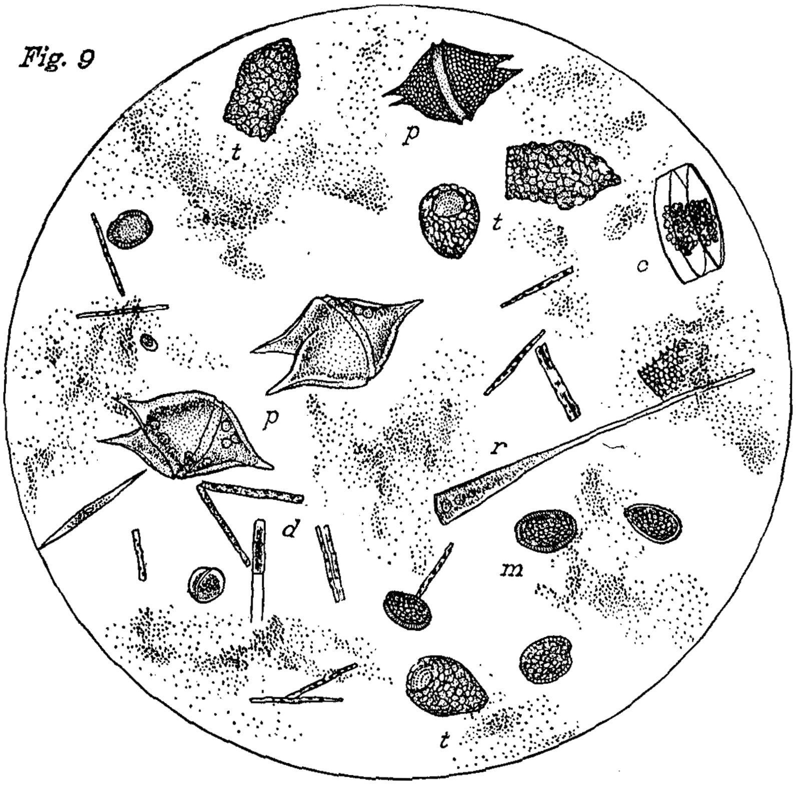


*Fig. 10*

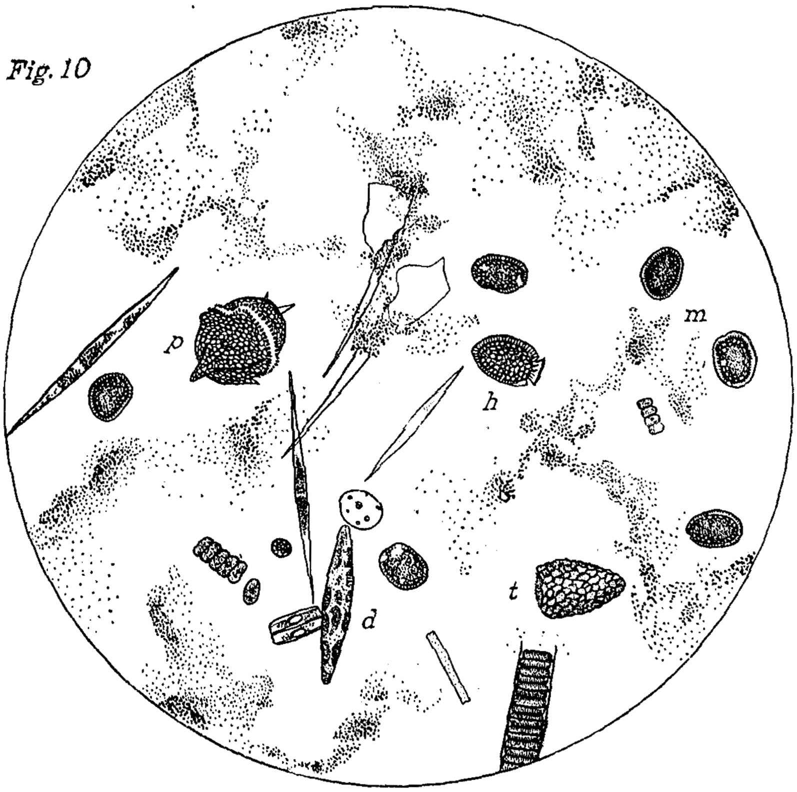


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*Fig. 11*

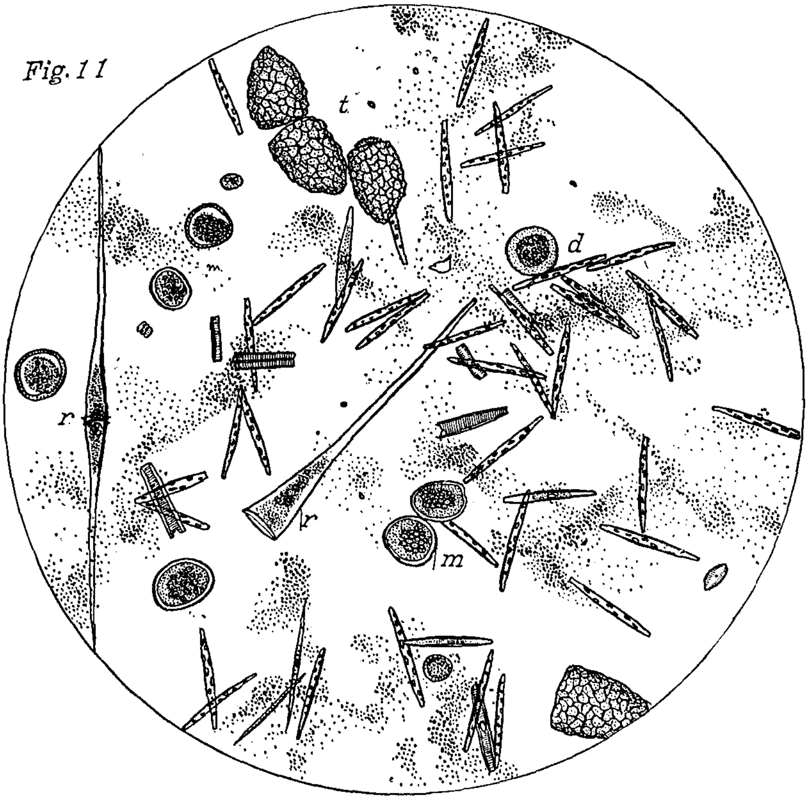


*Fig. 12*

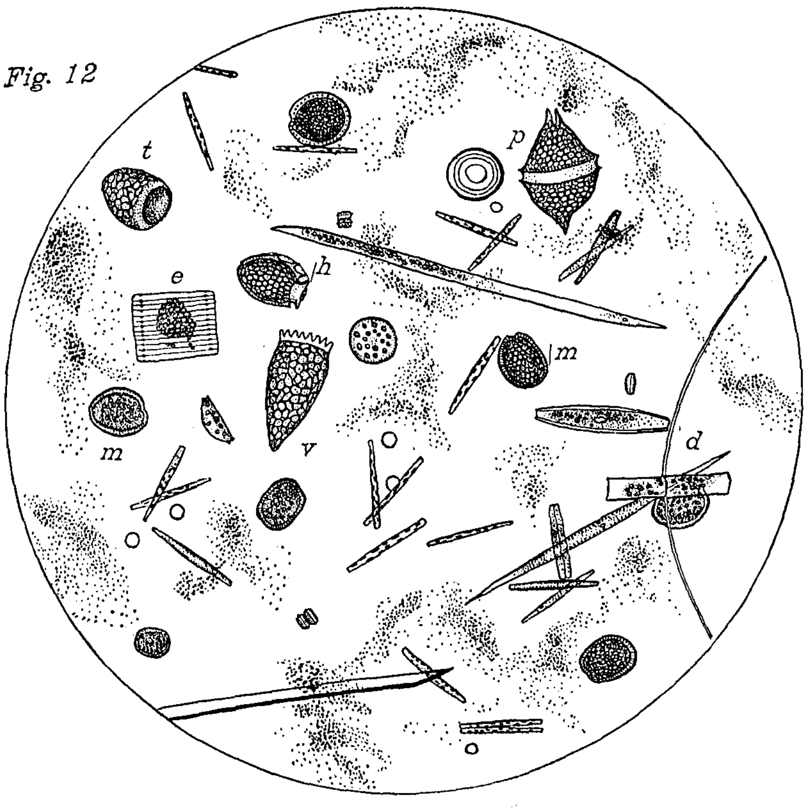


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Fig. 13

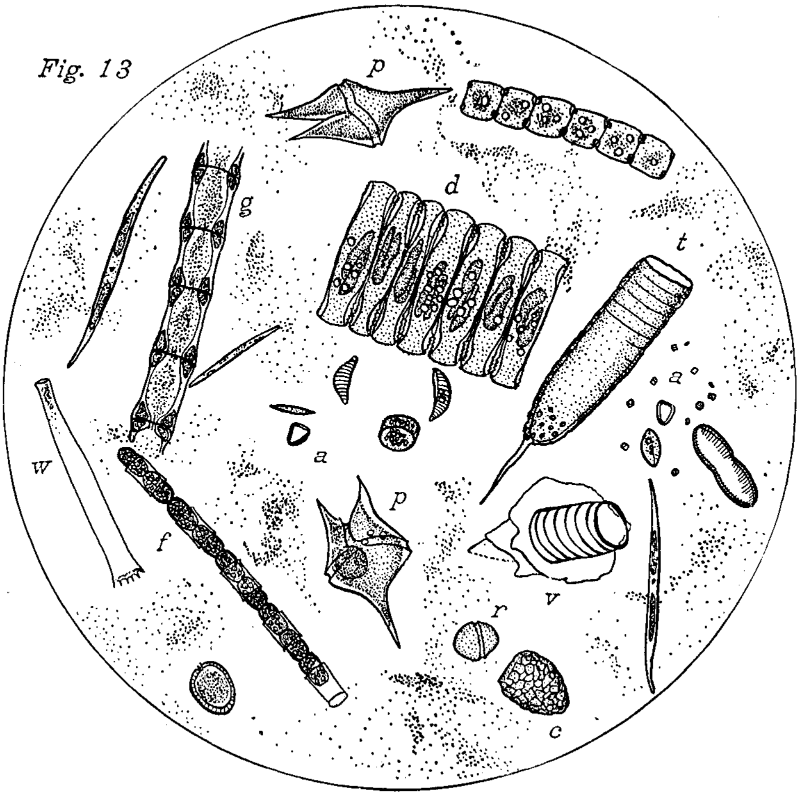


Fig. 14

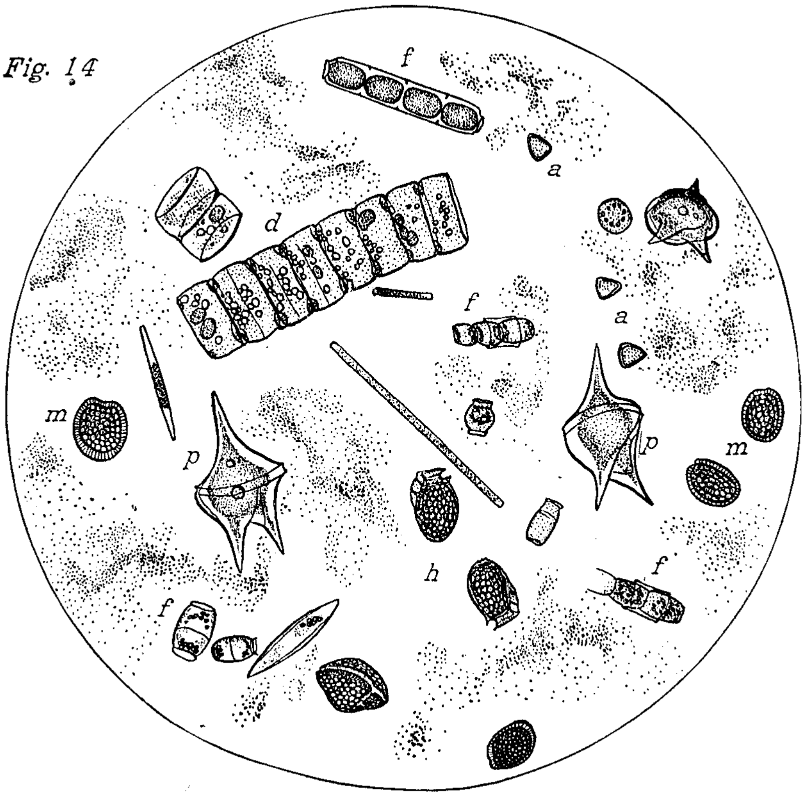


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*Fig. 15*

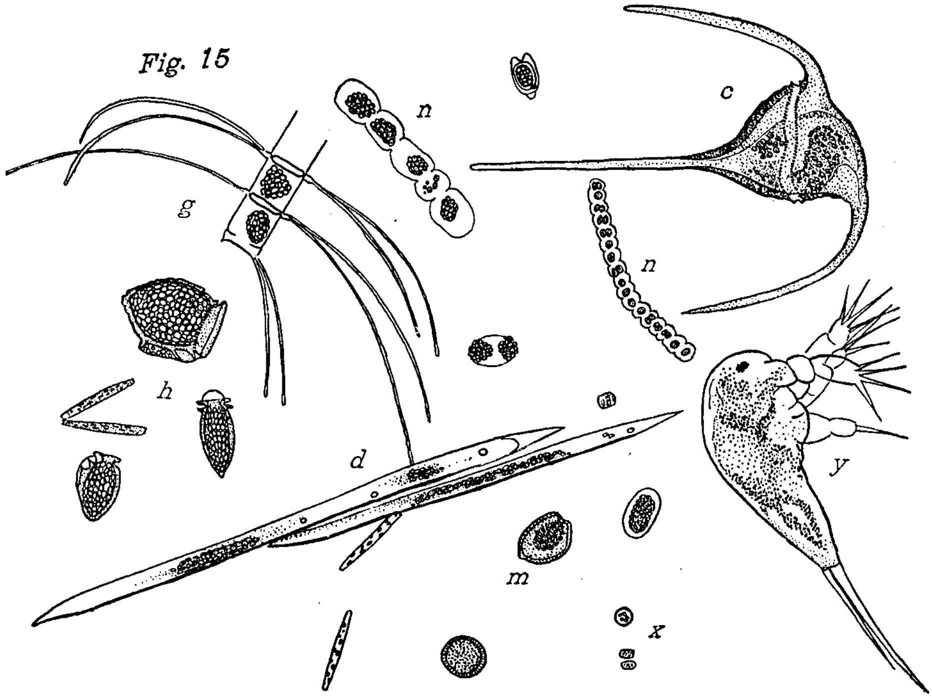
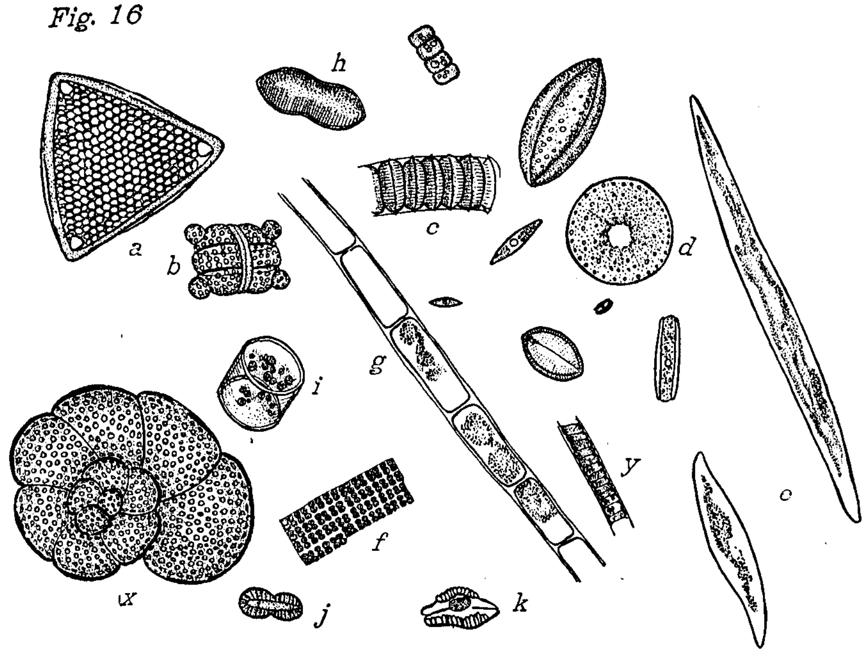



*Fig. 16*

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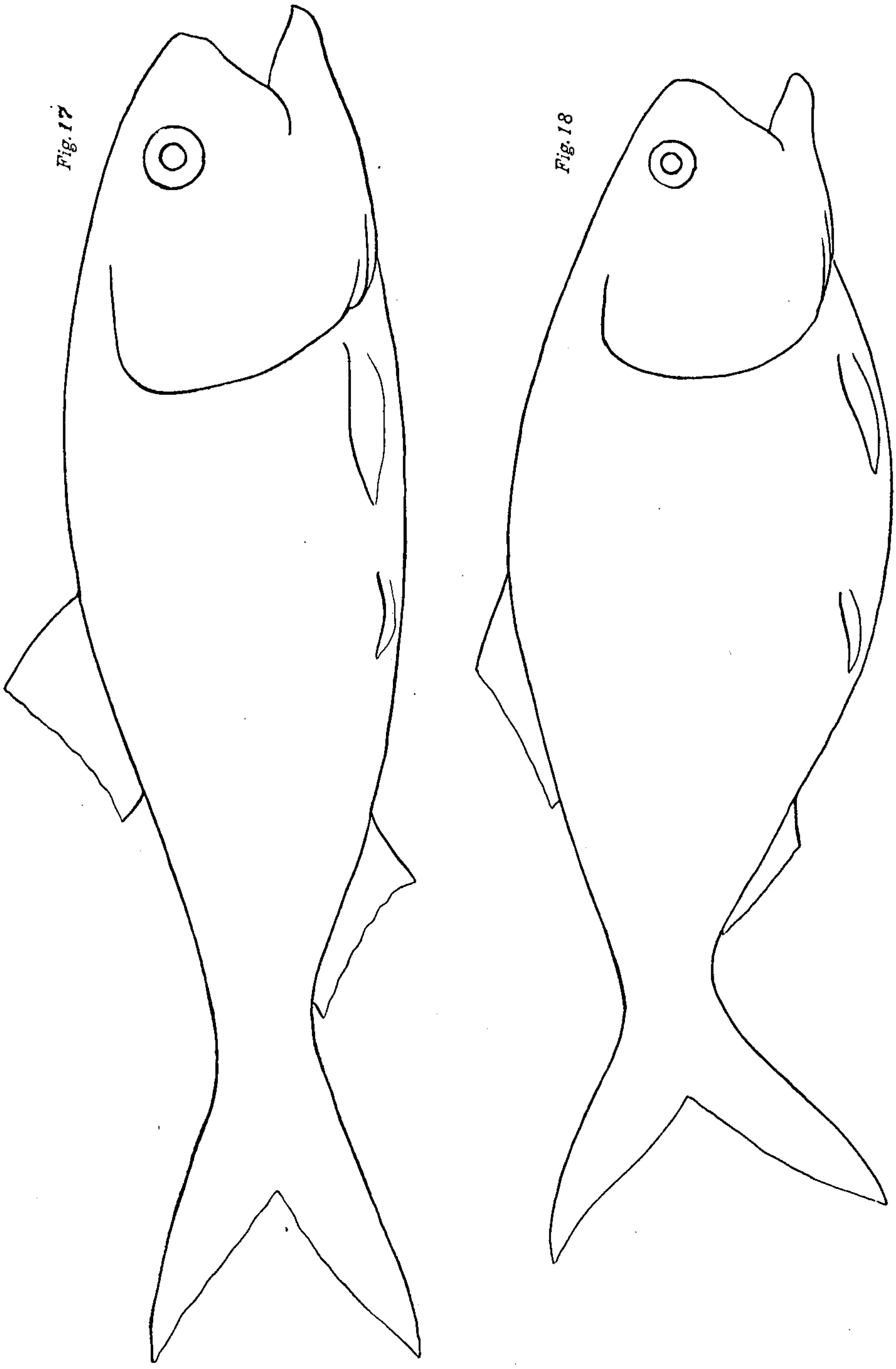


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